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No. 1. — *Reports on the Results of Dredging, under the Supervision of* ALEXANDER AGASSIZ, *in the Gulf of Mexico* (1877–78), *in the Caribbean Sea* (1879–80), *and along the Eastern Coast of the United States during the Summer of* 1880, *by the U. S. Coast Survey Steamer "Blake,"* LIEUT.-COMMANDER C. D. SIGSBEE, U. S. N., *and* COMMANDER J. R. BARTLETT, U. S. N., *Commanding.*

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XXX.

Report on the Holothurioidea, by HJALMAR THÉEL. *With one Plate.*

THE following list not only enumerates the deep-sea Holothurians which were dredged during the Blake expeditions, but contains also several other shallow-water forms brought home from different localities of America, principally by the Hassler Expedition, and now in the Museum of Comparative Zoölogy of Cambridge. Referring to my report on the Challenger Holothurioidea, to which this list properly may be considered as an Appendix, I have nothing of importance to add with regard to general conclusions.

Deima Blakei, n. sp.

Figures 1, 2.

Three of the specimens present the greatest similarity with *Deima validum*, while the remaining forms differ in a marked manner, having a certain degree of variability and asymmetry in the number of pedicels and processes. The three first-mentioned forms have eleven pedicels on each side of the ventral surface, the posterior pair being very minute and placed behind the anus, which is completely ventral in position. Immediately in front of the anus a pair of minute pedicels run out from the odd ambulacrum, which is almost naked or possesses one or two rudimentary almost inconspicuous appendages. Along each side of the body, above the pedicels, a row of six large conical processes is situated ; the dorsal surface bears, in addition, five or six pairs of such processes.

The other specimens, on the contrary, are not of such evident symmetry, the number of processes and pedicels being more variable, and the processes being much more flexible, almost like those in *Oneirophanta mutabilis*.

With regard to the deposits, all the specimens resemble the last-mentioned species, to which they also bear a strong resemblance regarding the shape of the genital tubes. According to the shape of the deposits, *Deima Blakei* has a much thinner and more flexible integument than *Deima validum*. Considering the obvious agreement with both Deima and Oneirophanta, I think the Blake specimens properly may be regarded as transitional forms combining these two genera. In external appearance, in the arrangement of the pedicels and processes, in the shape of the tentacles, etc., they closely remind one of the genus Deima.

Habitat. St. Vincent; depth, 573 fathoms; six specimens. Lat. 17° 28′ 30″ N., Lon. 77° 30′ W. (1880); depth, 610 fathoms; one specimen.

Orphnurgus asper, Théel.

Habitat. Guadeloupe; depth, 583 fathoms. A single specimen.

Euphronides depressa, var. minor, n.

All the specimens are greatly deformed. The largest attains only 150 mm. in length. The azygos dorsal appendage is, as a rule, small.

Habitat. Lat. 39° 38′ 20″ N., Lon. 70° 56′ W.; depth, 1241 fathoms; numerous very badly macerated specimens. Lat. 24° 33′ N., Lon. 84° 23′ W.; depth 1920 fathoms; several specimens. Lat. 41° 24′ 45″ N., Lon. 65° 35′ 30″ W. (1880); depth 1242 fathoms; one specimen.

(?) Benthodytes typica, Théel.

All the specimens are badly macerated and deformed, and in such a state of preservation as to render a closer examination impossible. As a rule, all the Psychropotidæ change very considerably when preserved in alcohol, and, in order to understand their organization and external appearance, it is quite necessary to see them living.

Habitat. Martinique; depth 1030 fathoms; numerous specimens. Lat. 24° 33′ N., Lon. 84° 23′ W.; depth 1920 fathoms; numerous specimens. Lat. 24° 30′ N., Lon. 88° 58′ W.; depth 1568 fathoms; several specimens. Lat. 19° 7′ N., Long. 74° 52′ W.; depth 1200 fathoms; two specimens.

Benthodytes assimilis, n. sp.

The species presents the greatest similarity with *Benthodytes sanguinolenta*, and differs from it only in some minute features, which possibly may

prove not to be of specific value. But considering the differences which really exist with regard to the outer appearance, and taking into consideration, that the deposits were dissolved in the types brought home by the Challenger expedition, I propose to refer it, for the present at least, to a new species.

The Blake specimen differs from *Benthodytes sanguinolenta* in being devoid of the transverse ventral row of papillæ situated immediately behind the crown of tentacles; the position of the anus is more ventral, and it carries only a very few slender dorsal processes, which seem to be confined to the two ambulacra alone. The madreporic canal appears to open exteriorly (?). The integument is rather rough from numerous larger and smaller deposits, which consist of four curved arms and a smooth central spine directed outwardly; each of the four arms generally bears a large process directed outwardly and a few smaller ones. In the ventral perisome, the deposits are more irregularly formed, and have the shape of unbranched rods and three- or four-armed bodies. Thus the deposits of this species closely resemble those of *Euphronides depressa*.

Habitat. Bequia; depth 1591 fathoms. One specimen, 220 mm. long and 53 mm. broad.

Benthodytes sp. (?).

The very defective state of the specimens at my disposal renders a detailed examination impossible. They seem to bear the closest resemblance to *Benthodytes abyssicola*. There appear to be fifteen tentacles. The dorsal ambulacral appendages are few and minute. The deposits present themselves as scattered, very large and robust four-armed spicules with a long spinous central spine, the extremity of which is usually split into two or three spinous tops, giving to the surface of the skin a remarkable roughness. The central spines are almost visible to the naked eye.

Habitat. Bequia; depth 1507 fathoms; three very incomplete specimens.

Pælopatides Agassizii, n. sp.

One of the largest specimens has the following measurements: length 270 mm.; breadth 120 mm.; height varying between 5 and 10 mm. The body is thus very depressed, almost flat, and very broad; its anterior and posterior ends are obtusely rounded or truncated. The pedicels are only present on the odd ambulacrum, where they form a thin double row over three fourths of its length; the anterior fourth of the odd ambulacrum is naked. The thin wide brim, which surrounds the body and reaches a breadth of about 40 mm., is pierced by a number of canals which branch off from the two ventral lateral ambulacra, cross the brim, and run out in very minute papillæ situated in the margin of the brim. These papillæ form a simple row in

the margin of the brim round the body, and are scarcely visible to the naked eye. The dorsal papillæ are minute, few in number, and probably confined to the ambulacra alone. The mouth is ventral in position, and the anus dorsal. There are twenty (?) tentacles. The color is bluish violet.

The deposits are scattered, and consist of very regularly formed three-armed bodies, with smooth nearly straight arms forming equal angles with one another and having the ends slightly enlarged and pierced with one or several holes; a long central simple column directed outwardly runs out from the centre of the body and terminates in some minute spines. The calcareous ring is evidently absent or dissolved. Two Polian vesicles 50 mm. long are present. Each of the longitudinal muscular bands is divided into two. The respiratory trees are long and more developed. A bundle of long slender genital tubes is situated on each side of the dorsal mesentery.

Habitat. Lat. 39° 43′ N., Lon. 10° 55′ 25″ W. (1880); depth 1002 fathoms; two specimens. Lat. 38° 16′ 45″ N., Lon. 73° 10′ 30″ W. (1880); depth 1186 fathoms; one specimen. Lat. 39° 38′ 20″ N., Lon. 70° 56′ W. (1880); depth 1241 fathoms; two specimens.

Stichopus Pourtalesii, n. sp.

On account of the very defective state of the specimens, it is almost impossible to get an exact idea of their true shape. So far as I can observe, they resemble in all respects *Stichopus natans* of Sars, except that the ventral surface appears to have two kinds of pedicels: small ones, like those of *Stichopus natans;* and very wide, wart-like ones, which seem to be placed along the sides of the body. By means of these warts the animals adhere firmly to rocks and stones, so that it seems almost impossible to obtain a perfect example. The deposits resemble those of *Stichopus natans*, Sars, but possibly the spire bears longer, more numerous spines on the four vertical rods. Considering the very incomplete state of all the specimens, it is probable that other differences also exist between this species and that of Sars, but for the present I cannot find any other than the large remarkable wart-like feet which *Stichopus Pourtalesii* possesses.

Habitat. St. Kitts (1878–79); depth 208 fathoms; fragments of several specimens. Grenada (1878–79); depth 291 fathoms; fragmentary specimens. Guadeloupe (1878–79); depth 734 fathoms; fragments. (Barbados 1878–79); depth 209 fathoms; fragments. Lat. 18° 20′ 30″ N., Lon. 87° 16′ 40″ W. (Bartlett, 1880); depth 600 fathoms; one specimen.

Stichopus Johnsoni, n. sp.

In a contracted state, the animal attains a length of 150 mm. The color is yellowish brown. There are twenty tentacles of the same size and shape. The ventral pedicels are not crowded, and they do not seem to form any well-

marked longitudinal series. The dorsal papillæ are scattered, and of two kinds : partly situated on rather large conical warts, and partly running out directly from the surface of the skin. The papillæ situated on warts form a simple row along each side of the body, about six in each row, and are besides found scattered irregularly over the rest of the back, though they appear to belong principally to the ambulacra. Scattered among these warts, the small papillæ are visible. A single Polian vesicle, 20 mm. long, is present. A thin bundle of long, slender genital tubes is situated on each side of the dorsal mesentery.

The deposits consist of tables and buttons. The disks of the tables are rather large, with a smooth or uneven margin, and are, as a rule, pierced with numerous holes, which form several peripheric circles. The disks of the ventral tables are smaller, and provided with fewer holes, which often form only a simple peripheric circle. The spire is built up of four rods and one transverse beam, and terminates in several teeth; usually some teeth are placed also on the rods themselves and the transverse beam, so that a side view often presents two crowns of teeth. The upper quadrangular opening of the spire is often closed by a complete or incomplete cross. The buttons are smooth, elongate, often asymmetrical or incomplete, and they are always pierced with more than three pairs of holes; usually one side of the buttons is more developed than the other.

Habitat. Five miles south of Santa Barbara (Cal.); depth 22 fathoms; a single specimen.

(?) Stichopus natans, Sars.

Habitat. St. Kitts (1878–79); depth 208 fathoms; some very imperfect specimens.

(?) Stichopus fuscus, Ludwig.

The specimen seems to agree in all respects with the description of Ludwig, with the exception of the dorsal papillæ, which have not been satisfactorily mentioned by Ludwig. In the specimen from San Diego all the papillæ are placed on low, wide warts, which are scattered over the dorsal ambulacra as well as interambulacra, so that they do not present an arrangement in rows, except along each side of the body, where they form a simple row. The C-shaped deposits appear to be thinly distributed, and the tables are small and terminate in 20 to 28 teeth; the margin of the disk of the tables is smooth, and perforated with a complete or incomplete circle of peripheric holes. The short spire is composed of four rods and one transverse beam.

Habitat. San Diego, California (Hassler Exp.). One specimen, 170 mm. long.

Holothuria Verrilli, n. sp.

The following description applies to the specimen dredged at St. Vincent. The body is ovate. The tentacles, probably twenty, are drawn inside the body. The ambulacral appendages consist of small pedicels, scattered over the body; they are rather distant on the greater part of the ventral middle line, and more closely packed along the lateral ventral ambulacra, and especially on the posterior portion of the ventral surface. They are not arranged in rows. The integument is very rough from numerous crowded tables, which are of varying size, some being very solid and robust, others of a more delicate structure. The rounded or angular disks of the tables are always pierced with a large central hole, surrounded by a single or several crowns of peripheral holes. The spire is, as a rule, built up of four rods and one or two transverse beams, and terminates usually in four rather long teeth, each provided with spines of considerable size; the spire is rarely built up of more than four rods. The specimen is whitish. The interior structure does not present any differences from that usual in other species of this genus.

The variations with regard to the tables appear to be considerable. In two of the specimens from Dominica, the spire often, but not always, terminates in four smooth teeth; in others, for instance those from Barbados and Grenada, the top of the spire has a very irregular aspect, from numerous longer or shorter teeth, which are placed not only round the opening of the top itself, but also on a cross-like rod which covers this opening.

Habitat. St. Vincent (1878–79); depth 464 fathoms; one specimen 110 mm. long. Dominica (1878–79); depth 611 fathoms; one gigantic specimen, 230 mm. long. Dominica (1878–79); depth 982 fathoms; two specimens. Lat. 17° 30′ N., Lon. 79° 14′ W. (1880); depth 555 fathoms. Lat. 18° 20′ 30″ N., Lon. 87° 16′ 40″ W. (1880); depth 600 fathoms; two specimens, 230 mm. long. Barbados (1878–79); depth 399 fathoms; one specimen. Grenada (1878–79); depth 416 fathoms; one specimen. Grenada (1878–79); depth 955 fathoms; one specimen.

Holothuria Murrayi, Théel.

Habitat. Guadeloupe (1878–79); depth 769 fathoms; two specimens.

Holothuria lactea, Théel.

Habitat. Lat. 41° 33′ 15″ N., Lon. 65° 51′ 25″ W.; depth 810 fathoms; numerous specimens, which differ from those brought home by the "Challenger" only in the fact that the spire of the table often terminates in a simple long spine. Lat. 39° 43′ N., Lon. 70° 55′ 25″ W. (1880); depth 1002 fathoms; numerous specimens. Lat. 38° 18′ 40″ N., Lon. 73° 18′ 10″ W. (1880); depth

922 fathoms; one typical specimen. Lat. 41° 29′ 45″ N., Lon. 65° 47′ 10″ W. (1880); depth 980 fathoms; one specimen. Lat. 18° 20′ 30″ N., Lon. 87° 16′ 40″ W. (1880); depth 600 fathoms; one specimen.

Holothuria arenicola, Semper.

Habitat. Charles Island, Gallapagos Archipelago (Hassler Exp., 1872). Five specimens.

Holothuria lubrica, Selenka.

Habitat. Mazatlan. Two specimens, agreeing in all respects with the description of Selenka. The ventral cylindrical pedicels are slightly more crowded than the small dorsal, conical papillæ. The curved rods of the integument are strongly spinous, especially towards the extremities.

Holothuria impatiens, Forskaal.

Habitat. Charles Island and James Island, Gallapagos Archipelago (Hassler Exp.). Four specimens.

Holothuria imitans, Ludwig.

One specimen is cylindrical, and measures 90 mm. in length and 12 to 14 mm. in breadth; the other two are more contracted, of an oval form, and have a length of 70 mm. and a breadth of 25 mm. The color is dark grayish or reddish brown on the back, and lighter on the ventral surface; the pedicels and papillæ are light. The anus is surrounded with five small groups of minute papillæ. In one of the specimens the ventral pedicels are distinctly arranged in four series, one along each side and two along the odd ambulacrum, each series containing about four pedicels in breadth. The dorsal papillæ are minute, smaller than the pedicels, and scattered without order. There are twenty tentacles.

The tables closely resemble those described by Ludwig, but he has drawn them with the upper part undermost, as I suggested in my report on the Challenger Holothurioidea. Thus, the tables are completely devoid of disks, and their spire carries at its outward end four double teeth. The rounded or truncate inward end of the spire also bears some spines. No other deposits are to be found in the body-wall itself, but the ambulacral appendages are supported by large, slightly flattened rods, which carry a series of prominences along each side; these prominences are often united with their ends, so that the rods themselves appear to have a series of holes along each side, just as is found in the rods of *Holothuria surinamensis*, Ludwig.

Habitat. Panama (Hassler Exp., 1872); three specimens.

Holothuria Marenzelleri, Ludwig (var.?).

Although there exist some differences between our specimens and those described by Ludwig, still I refer them to the above species on account of the great similarity which I find to exist in several essential structural points. All the specimens are of a dark brown color, and the largest reaches a length of 110 mm. in a contracted state. There are twenty tentacles. The anus is round. Contrary to what seems to be the case in the typic *Holothuria Marenzelleri*, the pedicels do not run out from warts, at least not the ventral ones; in some more contracted specimens, however, the dorsal pedicels give the impression of doing so. The dorsal pedicels do not seem to be true pedicels, but papillæ of a conical form, while the ventral whitish ones are longer, cylindrical, and provided with distinct light brown sucking disks. The ventral pedicels are possibly slightly more numerous than the dorsal papillæ. I have observed a low furrow along each side of the body, marking out the transition between the dorsal and ventral surfaces. The calcareous ring is of usual shape. Three larger and some smaller Polian vesicles are present. A single madreporic canal is to be found. The genital organ consists of a single bundle of slender, slightly branched tubes situated on the left side of the dorsal mesentery. The ampullæ of the dorsal and ventral appendages are distinctly visible on the inner surface of the skin.

The deposits consist of short rods, which, however, very seldom remain simple, but have the ends slightly dichotomously branched so that they have the aspect of an X; very often the branches of these deposits are united, the rods themselves thus becoming transformed into perforated plates or plate-like rods. A great part of the deposits also have the shape of small, very irregular, smooth plates, perforated with a few (two to ten) holes, and spinous in the uneven margin.

For my own part I must confess that most of those so-called species of Holothuria which are characterized by having calcareous rods or small plates in the skin resemble each other very closely, and that a revision of them is highly desirable. Thus, the specimens from the Galapagos Archipelago also bear a striking resemblance to *Holothuria lubrica*, Selenka.

Habitat. Charles Island and James Island, Galapagos Archipelago (Hassler Exp., 1872). Numerous large and small specimens.

Cucumaria californica, Semper.

A detailed examination of the specimens shows several differences from the type, but considering that Semper's specimen only attained half the size of the specimens at my disposal, and that they are dredged at the same locality, I must suppose that they represent the same species.

The body is ovate, and possesses ten nearly equal tentacles. The large pedicels form a double row along each ambulacrum; the interambulacra are

naked. The color is darker or lighter violet or brown; the pedicels are yellowish and the tentacles blackish. Probably the animal is dark in living state. The calcareous ring is devoid of posterior prolongations, and in a low state of development. The deposits consist of numerous thick, roundish, oval or elongate, irregular perforated plates, which, contrary to the figure drawn by Semper, often present uneven surfaces from the presence of low elevations or knobs. However, the plates not unfrequently seem to be quite smooth. The number of perforations is variable. The pedicels are supported by elongate simple or three-armed perforated spicules or rod-like plates, and possess a very fragmentary terminal plate. In one of the specimens the exterior layer of the perisome contains small, scattered, irregularly formed perforated spicules, which are either simple or irregularly three- or four-armed. These spicules, which are of much finer construction than the underlying plates, are probably dissolved in the remaining specimens. The specimen from Magdalena Bay appears to possess anal teeth (?).

Habitat. Mazatlan; three specimens. Magdalena Bay; one specimen.

Cucumaria dubiosa, Semper (var.?).

The specimens agree in all respects with the type described by Semper, except that no interradial pedicels are to be distinguished. Considering, however, the very striking similarity in every other respect, I can only refer them to the species of Semper. There is no doubt that *Cucumaria miniata* also bears the greatest resemblance to this species; a revision of all such forms which are characterized by possessing the same kind of deposits is highly desirable.

Habitat. Eden Harbor in the Strait of Magellan (Hassler Exp.); several specimens. Mayne Harbor in the Strait of Magellan (Hassler Exp.); one specimen. Lat. 37° 42′ S., Lon. 56° 20′ W. (Hassler Exp.); depth 44 fathoms; two specimens.

Echinocucumis typica, Sars.

Figure 3.

Some of the specimens, especially those brought home from Barbados and St. Kitts, are remarkable in having an almost completely spherical body with a highly reduced bivium, so that the oral and anal apertures closely approach each other. The specimens obtained at Barbados reach 15 mm. in diameter, and their whole appearance reminds one most strikingly of an Ascidian; the trivium is enormously developed; the mouth and anus are each situated in a small conical prominence on the upper part of the sphere. Otherwise they seem to resemble the Norwegian *Echinocucumis typica* in almost every detail. However, in the West Indian forms the pedicels seem, as a rule, to be smaller

and more scattered on the ambulacra, excepting towards the mouth and anus, where they appear to be much more crowded; two of the tentacles are very long, resembling in their retracted state long slender tubular sacs strengthened with crowded transverse calcareous spicules, and they appear to be almost unbranched. The close-lying plates render the body-wall very hard, rough, and brittle, and closely resemble those in the type described by Sars.

With regard to the shape of the body, the specimens from Barbados form a transition between the Dendrochirotæ and Rhopalodinidæ.

Habitat. Grenada (1878–79); depth 576 fathoms; one typical specimen. Off Morro Light (1878–79); depth 250–400 fathoms; one typical specimen. St. Vincent (1878–79); depth 464 fathoms; one specimen. St. Kitts (1878–79); depth 270 fathoms; four specimens. Lat. 24° 8′ N., Lon. 82° 51′ W. (1877–78); depth 339 fathoms; eight specimens. Barbados (1878–79); depth 209 fathoms; two specimens.

Echinocucumis asperrima, n. sp.

The body, like that of *Echinocucumis typica*, is curved; the ventral surface is considerably more developed and more convex than the dorsal. The body tapers strongly both towards the anterior and posterior extremity; the caudal portion is long, narrow, and tail-like. In the largest specimen, the body itself measures about 25 mm. in length and 17 mm. in thickness; the retracted anterior portion of the animal is 10 mm. long, and the tail 18 mm., so that the whole length becomes about 53 mm. When fully extended the length is probably considerably greater. The anus seems to be fringed by cylindrical papillæ and teeth (?). The hard, brittle glassy integument is filled up with large reticulate scales, which are visible to the naked eye, each scale being provided with a long, more or less eccentric spine, which gives to the skin an almost spinous aspect. A closer examination reveals that each scale is irregularly oval or elongate, and composed of several superposed layers of calcareous network; the spine, or rather spire, which is situated more or less near the margin of the scales, presents traces of having been composed of a network like that in *Echinocucumis typica*, but the perforations have disappeared, and the whole forms a more or less irregular cone; at the base of the spine some perforations are often found.

So far as I can see, the tentacles are like those of *Echinocucumis typica*. The calcareous ring is very minute and devoid of posterior prolongations. A single madreporic canal and one Polian vesicle are present.

The pedicels are very minute, so that it is difficult to detect them among the large spines of the deposits. They appear to be more scantily distributed than in *Echinocucumis typica*, but belong evidently to the ambulacra alone; towards the extremities of the body, the pedicels are more easily distinguished. They are supported by curved transverse rods.

Habitat. Lat. 17° 55′ N., Lon. 76° 41′ 20″ W. (1878–79); depth 150

fathoms; one specimen. Lat. 22° 9′ 30″ N., Lon. 82° 23′ W. (1877–78); depth 158 fathoms; one specimen. Frederikstad (1878–79); depth 180 fathoms; one specimen.

Thyone scabra, Verrill.

The length of the larger specimen in the retracted state is about 90 mm. The anus possesses fine calcareous teeth. The pedicels are cylindrical, slender, rigid, and present in great number; they attain a length of about 2 mm. The calcareous ring closely resembles that in *Thyone fusus*. A single Polian vesicle and one madreporic canal are present. The calcareous tables of the perisome remind us slightly of those in the above-mentioned species, but the disks are much more irregular, and pierced with a greater number of holes (sometimes as many as twenty) of nearly equal size. The species undoubtedly bears a striking resemblance to *Thyone fusus*, but differs in having a strongly curved body, and in that the posterior portion of the body is long and tapering; the tables are also different.

Habitat. Lat. 40° 1′ N., Lon. 70° 58′ W. (1880); depth 129 fathoms; several specimens. Lat. 38° 21′ 50″ N., Lon. 73° 32′ W. (1880); depth 197 fathoms; one specimen.

Thyone spectabilis, Ludwig.

Habitat. Patagonia (Hassler Exp.); numerous specimens. Off Bermeja Head, Lat. 41° 17′ S., Lon. 63° W.; depth 17 fathoms; several specimens.

Thyone Hassleri, n. sp.

The body in a contracted state is nearly cylindrical, slightly more tapering towards the posterior extremity, and measures about 120 mm. in length. The color is brownish, except the ends of the pedicels, which are whitish. The two ventral tentacles are much smaller than the remaining eight. The body-wall is rather thin, but hard in consequence of the close-lying deposits. In the three specimens at my disposal, the ambulacra are marked by a low, longitudinal furrow. The pedicels, which seem to be slightly larger and more closely placed on the ventral surface, and very sparsely scattered in the anterior portion of the body, are present on the ambulacra as well as the interambulacra; but they are possibly absent on a very narrow space along each interambulacrum. The deposits are very closely crowded, and consist principally of two kinds: small, rounded, discoidal, highly transparent bodies in several layers; and minute, scattered, perforated cups. The discoidal bodies, which are larger in the interior layer, resemble at first sight agglomerations of drops of oil; generally, they are not perforated, though they not unfrequently have one, two, or four holes. Those in the inner layer of the perisome are usually without

holes. The cups are often irregular and not very well developed, occurring in several stages of growth. A complete cup is built up of a cruciform rod with the curved arms united by a rim provided with several knobs. Sometimes the cups almost form spheres.

At the posterior end of the body, the skin is filled up with irregular large plates, perforated with numerous holes; these plates are partly simple, partly composed of several superposed layers, so that each plate has the aspect of a thick irregular network. The posterior end of the body also feels very rough and hard to the touch. The anus is devoid of teeth.

The pedicels have a small, more or less reduced terminal plate, but are devoid of true supporting rods. The strong retractors are attached slightly in front of the middle of the body. A single Polian vesicle and one madreporic canal are present. Each genital bundle is very well developed, and consists of numerous unbranched slender tubes. The calcareous ring is composed of ten simple pieces, devoid of posterior prolongations.

This species certainly bears a strong resemblance to *Thyone* (*Thyonidium*?) *lechleri*, Lampert, but differs mainly in the shape of the deposits and the calcareous ring.

Habitat. Sandy Point, Strait of Magellan (Hassler Exp.); three specimens.

Thyonidium molle, Selenka.

The tentacles vary greatly in number and size. The radial pieces of the calcareous ring are slightly prolonged and bifurcate posteriorly.

Habitat. Payta, Peru (Hassler Exp.). Several specimens.

Psolus operculatus, Pourtalès.

Figure 4.

In addition to the description of Pourtalès, the following may be mentioned. As a rule the odd ambulacrum is naked, except at the anterior and posterior extremities where a few pedicels are to be found; but in two specimens one or more pedicels are also placed at about the middle of that ambulacrum. The sole is strengthened by numerous close-lying deposits of a more or less marked symmetrical shape; they consist of solid oval or roundish slightly concave plates or cups, which usually are perforated with four holes, and have the margin more or less deeply undulated from low outwardly directed knobs. In addition to the symmetrical cups, others are present more or less developed and pierced with a varying number of holes.

The largest complete specimen in the collection measures 37 mm. in length, 24 mm. in breadth, and about 11 mm. in height. The smallest has only a length of 15 mm. In all the specimens I have seen, the mouth has five large triangular scales, which, however, do not cover the opening completely, but

leave a central space free; in consequence of the scales being obtusely rounded at their free angle, the naked central space of the mouth has an almost stellate shape; and in each angle of this space, which alternates with the free obtuse ends of the scales, a tooth-shaped free pointed end of an underlying scale becomes visible. These "teeth" are easily distinguishable in the smallest, as well as largest specimens. The anus is surrounded by small overlapping scales in such a manner that no true valves become visible. The scales are covered with minute rounded granules. The number of scales between the mouth and anus varies; in the largest specimen they are about ten. In all specimens the pedicels form a double row round the sole, those in the exterior row piercing the margin of the body.

One of the largest specimens from Barbados has the following measurements: length 38 mm., breadth 32 mm., and height 25 mm. Consequently, it is not depressed, but almost hemispheric, and is covered with numerous grains placed upon the scales on the dorsal surface. These grains resemble very complicated tables, and consist of a concave perforated disk supporting an irregular elongate network with numerous small teeth in the free end. In addition to the grains, the exterior layer of the dorsal integument contains small, concave perforated cups, which carry numerous obtuse spines in the rim. I have not been able to observe such cups in the other specimens at my disposal, but they probably have been destroyed, together with the exterior layer of the integument. The sole of the above-mentioned large individual bears deposits which are often larger and more irregular than is the case in the typical specimen.

Among the small typical specimens obtained at Sand Key, three are remarkable in having anal and oral valves arranged just as in *Psolus tuberculosus*, and in possessing only about three scales between the oral and anal valves. It seems very probable that these specimens belong to another species.

Habitat. Sand Key; depth 110 to 150 fathoms; numerous typical specimens. Barbados (1878–79); depth 82 to 103 fathoms; three small specimens, about 15 mm. long, and one larger specimen, 38 mm. long and 32 mm. broad.

Psolus tuberculosus, n. sp.

Figure 5.

As is seen from the figures, the exterior appearance of this species is very characteristic. The specimens dredged at Sand Key are the largest, and may be considered as types. They measure 30 mm. in length, 16 mm. in breadth, and 14 mm. in height. When the animals are fully extended, these measurements become slightly different. The mouth is closed by five large triangular valves, which form together a very regular pentagonal shield; the anus is also closed by five small valves, which have the free angle rounded, and which form together a small, more rounded pentagon, or anal shield. The dorsal surface is very hard and rough from large scales, which appear to be placed side by side

and to overlap very little; the marginal plates are, as usual, of minute size. The scales bear numerous rounded granules, and, in addition, a very large central process or tubercle of conical form with rounded top. The valves and the marginal plates appear to be devoid of such tubercles. The largest tubercles attain a length of nearly 3 mm., and are placed one in each angle of the oval pentagonal shield. The anal pentagon has a rather prominent tubercle at each angle. The ventral sole is surrounded by a double row of pedicels, those in the exterior row perforating the margin of the body. Anteriorly, where the body is more contracted, the inner row appears to be double, but this evidently depends upon the contraction. The sole is strengthened by crowded large irregular plates of various size, perforated by numerous holes (the largest plates have as many as fifty holes or more) and provided with numerous rounded knobs; the ends of the knobs are sometimes united, thus constituting an irregular network on the exterior surface of the plates themselves. All the remaining forms are comparatively small, the smallest only 7 mm. long; as a rule, all the small specimens I have seen have more numerous and densely crowded tubercles, which generally resemble rather long spines, while the small rounded granules, on the contrary, are not so abundant, or may be even absent.

Habitat. Off Sand Key (1877–78); depth 50 fathoms; one slightly contracted specimen. Barbados (1878–79), depth 103 fathoms, two small, contracted specimens; depth 84 to 125 fathoms, one small specimen; depth 73 fathoms, three small specimens; depth 94 fathoms, two minute specimens 7 mm. long. Barbados (Hassler Exp.), depth 100 fathoms; several small specimens. Dominica (1878–79), depth 118 fathoms; one specimen, 15 mm. long. Lat. 25° 33′ N., Lon. 84° 21′ W. (1877–78); depth 101 fathoms; one specimen, 15 mm. long, 13 mm. broad, 8 mm. high. (?) Lat. 23° 52′ N., Lon. 88° 5′ W.; depth 95 fathoms; two specimens which possibly do not belong to this species.

Psolus Pourtalesi, n. sp. (?).

Figure 6.

All the specimens, which are of about the same size (30 mm. long, 20 mm. broad, and 6 mm. high at the mouth), are remarkable in being very depressed and flattened. With regard to the arrangement of the scales, and their size, they evidently resemble *Psolus incertus* of Théel and *Psolus peronii* of Bell, but they differ from these two species in several respects, especially in the shape of the body. As will be understood from the figures, *Psolus Pourtalesi* has numerous small, almost smooth scales, and is totally devoid of any oral and anal valves. The pedicels form a double row round the sole, those in the exterior row perforating the margin of the body. The odd ambulacrum is naked, or possesses a few pedicels in its anterior and posterior parts. The sole is strengthened with thinly scattered cruciform bodies, the arms of which often

are dichotomously branched and united with one another, so as to give origin to small, smooth perforated plates. There is no doubt that *Psolus Pourtalesi* is nearly allied to *Psolus squamatus*.

Habitat. Lat. 41° 24′ 45″ N., Lon. 65° 35′ 30″ W. (1880); depth 1242 fathoms; ten specimens.

Psolus braziliensis, n. sp.

Figure 7.

The body is like that in *Psolus phantapus*. The length, including the extended mouth, is 32 mm. The color is whitish. Two ventral tentacles are always much smaller than the eight remaining. The ventral rectangular sole carries three series of pedicels, the two lateral composed of about four rows, the middle of only two. Anteriorly and posteriorly the series run together. The exterior row of each lateral series is placed in the margin of the body. The dorsal body-wall is rather soft and covered with scales, which overlap very little. The mouth is not closed by valves, but by a series of elongate triangular scales with a very acute free angle; the anus is closed by similar smaller and more irregular scales. Outside of the scales, the dorsal perisome contains minute conical cup-like tables, and large, elongate conical table-like deposits made up of a more or less irregular network with the free end spinous. The sole is strengthened by small, scattered, smooth plates with an uneven margin and perforated by four or more holes.

Scattered among the dorsal deposits small, highly reduced "pedicels" are found, which are strengthened by a small but very well marked perforated terminal plate, and by well-developed irregular plates. There is no doubt that these are true pedicels, and thus it is a very interesting fact, that some species of Psolus have retained the dorsal pedicels, though in a very rudimentary state. The scales seem to present some larger pores, through which the pedicels communicate with the ambulacral system (?).

Habitat. Porto Seguro; two specimens.

Psolus, sp. (?).

The body, which has a length of 12 mm., is very flattened and covered with scales on the dorsal surface; these decrease considerably in size towards the oral and anal openings, which consequently are completely devoid of valves. The general appearance of the body closely resembles that of *Psolus Pourtalesi*. The pedicels form a double row round the sole, the exterior row being placed in the margin of the body. The odd ambulacrum is naked. The sole is strengthened with small plates of a more or less symmetrical appearance; the most symmetrical are oval, with four holes, and twelve knobs or rounded prominences arranged in the margin; in addition, the surface itself of the

plates bears a few knobs. The plates themselves are, however, rarely so symmetrical; they mostly have more or fewer holes and knobs.

The most characteristic feature of this animal is that each dorsal scale bears one or several slender flexible cylindrical appendages, which are supported by a peculiar calcareous skeleton, composed of small crowded perforated plates or cups. Unfortunately, the material is too scanty to allow any detailed examination, or to decide whether these appendages have any communication with the water-vascular system.

Habitat. Lat. 25° 35′ N., Lon. 84° 21′ W. (1877–78); depth 101 fathoms; one very defective specimen.

Trochostoma Blakei, n. sp.

Figure 8.

The body is ovate, the anterior extremity truncated and the posterior suddenly tapering into a narrow tail or caudal portion. There are fifteen (?) tentacles. The anus is devoid of anal teeth (?). The color is whitish or grayish. The length of the body itself is about 68 mm., and that of the tail 7 mm. The tail is doubtless longer when fully extended. The integument is thin, almost transparent, but rough from numerous close-lying tables, which have a peculiar shape. They consist of a small disk, which as a rule is pierced with three comparatively large holes and has a more or less marked trilobate rim. The disk supports a very long simple and slender column, which at the base appears as composed of three rods. The end of the column is usually divided into three obtuse slightly curved teeth, or it is slightly enlarged and surrounded by a circlet of small hooks directed downward. The disks of the tables rarely have more than three holes; but when that is the case, three of the holes are always larger. In the tail, the tables have an elongate fusiform disk, which has about four holes in the enlarged centre and carries a spire made up of three rods and terminating in several spines. No other deposits are to be observed. The species is nearly related to Marenzeller's *Trochostoma arcticum*.

Habitat. Grenada (1878–79); depth 955 fathoms; one specimen.

Trochostoma antarcticum, Théel.

The specimens agree most fully with the Challenger specimens. The deposits consist only of tables, characterized by their long spire, which as a rule is composed of three parallel rods united by numerous transverse beams; the ends of the three rods are bipartite or tripartite. No true wine-colored deposits are visible, but several of the tables themselves have begun to change in color, so that they in some places present a yellowish brown aspect ; immediately in the neighborhood of these yellowish portions of the tables, some

small colored grains are visible, but these grains are never found except in connection with such deformed tables. In *Ankyroderma Marenzelleri*, Théel, the deposits also seem to undergo similar changes in color. I am much inclined to think that the presence or absence of wine-colored bodies cannot be accepted as specific characters.

Habitat. Lat. 24° 8′ N., Lon. 82° 51′ W. (1877–78); depth 339 fathoms; three specimens.

Trochostoma arcticum, Marenzeller, var. parva, n.

This form evidently bears the greatest resemblance to *Trochostoma arcticum*, but some minor differences exist, in consequence of which I propose to conconsider it as a variety. The fifteen tentacles have only a single short branch on each side. The body-wall is very thin, but rough from the scattered tables. The tail of the animal is destroyed, but the remaining portion of the body measures about 60 mm. The color is yellowish gray. The calcareous ring possesses five bipartite posterior prolongations. The scattered tables have an irregular disk, which is pierced with a varying number of large holes (usually few in number) and provided with prolongations or processes running out from the circumference of the disk. The disk supports a spire, which is irregularly spinous especially towards the free end, and composed of three rods, which are transversely united at several points.

I have examined two other specimens dredged at the same station, the largest of which attains a length of only 30 mm. Among the usual tables I have found some minute ones resembling those of *Trochostoma antarcticum*. Théel. This variety probably combines the extremes living in the arctic and antarctic seas.

Habitat. Grenada (1878–79); depth 416 fathoms; one specimen.

Trochostoma arcticum, Marenzeller, var. cœruleum, n.

This variety is distinguished from the northern form only by the abundance of pigment in the skin, which gives to the animal a bluish-violet color. Possibly also the disks of the tables are larger and more regularly formed. The tentacles have only a single pair of short branches near the top.

Habitat. Grenada (1878–79); depth 553 fathoms; one specimen, about 80 mm. long.

Caudina arenata, Gould, var. armata, n.

So far as I can observe, the specimens agree in all respects with those described by Selenka, Semper, and Marenzeller, except in the shape of the deposits. The body itself of the largest specimen measures about 50 mm. in length, and the narrow caudal portion is 35 mm. long. The fifteen tentacles

have each two pairs of minute branches or digits. The calcareous ring has five bipartite prolongations.

The very crowded deposits consist of irregularly formed tables, which deviate from those described by Semper, etc. in having much larger disks and a spire made up of only three rods, in consequence of which I propose to refer the Blake specimens to a variety. In general, the disks of the tables are large, smooth, of an irregular shape with uneven margin, and pierced with numerous holes. They often have an irregular triangular or quadrangular form, with twenty or more holes. The spire is composed of three irregularly spinous rods, united by a few (two or three ?) transverse beams. So far as I can understand from the descriptions hitherto made, the spire in the typical specimens should be composed of four rods.

Habitat. Lat. 35° 44′ 40″ N., Lon. 74° 40′ 20″ W. (1880); depth 898 fathoms ; three specimens. Lat. 41° 24′ 45″ N., Lon. 65° 35′ 30″ W. (1880); depth 1242 fathoms ; two specimens.

Ankyroderma affine, Danielssen & Koren (var.).

In the specimen dredged at St. Vincent, a few light wine-colored bodies are present. On the contrary, I have not been able to detect a single one of those colorless bodies which have been figured and described by Danielssen and Koren (compare Figs. 26 and 27 in their report), and I must confess that these bodies appear to me to be nothing else than artificial products owing to preservation in alcohol.

Among the "tables" I have observed a few very scattered, minute perforated plates supporting a very long spine, which carries at the top a crown of hooks, like those found by me in *Trochostoma antarcticum*. The anchors always have a discoidal, perforated base. Contrary to what is observed in *Ankyroderma Jeffreysii* (var.), I never found the fusiform bodies except at the extremities of the body.

Habitat. St. Vincent (1878–79) ; depth 464 fathoms; one specimen, 35 mm. long. Dominica (1878–79) ; depth 391 fathoms; one specimen.

Ankyroderma Jeffreysii, Danielssen & Koren (var.).

Some of the specimens have a marked violet color from more or less crowded wine-colored bodies, while others are almost colorless and devoid of such bodies. The anchors have a discoidal perforated base, just as I have found in *Ankyroderma Danielsseni*, which possibly may prove to be only a variety of *Ankyroderma Jeffreysii*.

Habitat. Lat. 41° 33′ 15″ N., Lon. 65° 51′ 25″ W. (1880); depth 810 fathoms; two specimens. Lat. 34° 39′ 40″ N., Lon. 75° 14′ 40″ W. (1880); depth 603 fathoms; one specimen. Lat. 38° 20′ 8″ N., Lon. 73° 23′ 20″ W.

(1880); depth 740 fathoms; one specimen. Lat. 33° 35′ 20″ N., Lon. 76° (1880); depth 647 fathoms; one specimen. Grenada (1878–79); depth 553 fathoms; two specimens.

Ankyroderma Agassizii, n. sp.

What especially distinguish this form from all hitherto known ones are the deposits, which form several superposed layers, so that the thin body-wall becomes rough and brittle. In the interior a continuous layer of large, smooth, irregularly rounded plates is to be found; these plates overlap each other by the edges, have a smooth but uneven margin, and are perforated with numerous holes, as many as sixty or seventy; the central are larger than the peripheral ones. Outside of these true plates we find other deposits, which, however, are not closely packed, but much scattered; they resemble the tables which are found in other forms of Ankyroderma, and consist of a rather large, irregular disk, perforated with a varying number of large holes and carrying a simple central spine. Here and there much smaller delicate tables may be found, which have a trilobate disk pierced with only three holes and resemble those found in *Trochostoma Blakei*. Scattered among these tables are situated the stellate bodies characteristic of the genus. They consist of three to six long spoonlike rods, arranged with the enlarged perforated end towards a common centre; the enlarged, slightly concave end is pierced with numerous holes, twenty-five to thirty or more. The anchors which are connected with these stellate bodies have the usual shape, their base being discoidal and perforated, and their symmetrical flukes slightly serrated.

The caudal portion of the body is strengthened by a thick layer of transverse fusiform rods, with the enlarged centre pierced by a few holes.

Otherwise, the body has the shape characteristic of the Molpodids.

The body itself is nearly cylindrical, about 60 mm. long, wider posteriorly, and decreasing slightly towards the anterior truncated end; at the posterior extremity it suddenly tapers into a narrow tail, which has a length of about 20 mm., so that the whole animal attains a length of about 80 mm. The tentacles are drawn within the body, their true shape and number being unknown. The color is light grayish inclining to violet. The radial pieces of the small calcareous ring bear a bifurcate posterior prolongation.

Another specimen was obtained at a depth of 1058 fathoms (from an unknown locality), which doubtless belongs to the same species. It has 15 minute tentacles and some small anal papillæ.

Habitat. Bequia (1878–79); depth 1507 fathoms; one specimen.

Synapta, sp. (?).

Habitat. Woman Key. One defective specimen, which probably is nearly related to Semper's *Synapta reticulata*.

Synapta, sp. (?).

From the defective state, a close examination is impossible. The handle of the symmetric anchors is dentate and the flukes serrated. The anchor-plates are rather large, rounded or oval, perforated with numerous holes, and at the slightly narrower truncate end, where the anchors are attached, resemble an irregular network. The margin of the plates is uneven from the presence of processes or spines, and spines are also present on the surface of the plates at the margin of the holes. Possibly the species is identical with *Synapta abyssicola*, Théel.

Habitat. Lat. 39° 25′ 30″ N., Lon. 70° 58′ 40″ W., depth 1394 fathoms; one incomplete specimen.

Chirodota rotifera Pourtalès.

The largest specimen, which measures about 75 mm. in length, has fifteen digits in each of the twelve tentacles (Ludwig only counted twelve digits). The wheel papillæ are principally placed on the interambulacra, but a few also occur on the ambulacra, and they are less numerous on the ventral surface than on the three dorsal interambulacra.

Habitat. Porto Seguro (Thayer Exp.); several specimens.

Chirodota contorta Ludwig.

Habitat. Port Gallant, Patagonia; numerous specimens.

List of Holothurids in such an imperfect Condition that their Examination is not possible.

Hab. Guadeloupe, depth 769 fathoms; one specimen.
" " depth 734 fathoms; fragments.
" " depth 878 fathoms; two fragments of an Aspidochirote.
" " depth 734 fathoms; a Molpodid.
" Dominica, depth 824 fathoms; fragments.
" " depth 982 fathoms; fragments.
" Martinique, depth 1030 fathoms; fragments.
" St. Vincent, depth 573 fathoms; one defective specimen, related to *Holothura Verrilli*.
" Bequia, depth 1591 fathoms; one specimen.
" " depth 1507 fathoms; fragments, probably of a Psychropotide.
" Ham's Bluff, depth 2376 fathoms; fragments of a Psychropotide.
" Grenada, depth 553 fathoms; fragments.
" Montserrat, depth 303 fathoms; fragmentary specimens.
" Off Havana, depth 100 fathoms; fragments probably of an Echinocucumis.
" St. Lucia, depth 116 fathoms; fragments of an Echinocucumis.
" Lat. 40° 1′ N., Lon. 70° 58′ W. (1880); depth 129 fathoms; an incomplete Chirodota.
" Lat. 24° 1′ N., Lon. 88° 58′ W. (1877–78); depth 1568 fathoms; fragments.
" Lat. 16° 42′ N., Lon. 83° 1′ W. (1878–79); depth 961 fathoms; fragments.
" Lat. 18° 51′ N., Lon. 83° 7′ W. (1880); depth 903 fathoms; fragments.

EXPLANATION OF THE PLATE.

Fig. 1. *Deima Blakei*, Théel, from above.
" 2. The same, from below.
" 3. *Echinocucumis typica*, Sars.
" 4. *Prolus operculatus*, Pourt.
" 5. *Prolus tuberculosus*, Théel.
" 6. *Prolus Pourtalesii*, Théel.
" 7. *Prolus brasiliensis*, Théel.
" 8. *Trochostoma Blakei*, Théel.

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No. 2. — *A Second Supplement to the Fifth Volume of the Terrestrial Air-Breathing Mollusks of the United States and Adjacent Territories.* By W. G. Binney.

The following pages contain a list of the Locally Introduced Species, the Universally Distributed Species, and the Central and Pacific Province Species, with such additional information relating to them as I have obtained since the publication in this Bulletin (Vol. XI. No. 8) of the first Supplement.

In a future Supplement, I propose to follow with the species of the Eastern Province.

Thus in this revision of the subject the species will be arranged geographically, not systematically.

LOCALLY INTRODUCED SPECIES.

Zonites cellarius, Müll.

Also found living in Portland, Oregon (Dore), and St. Louis.

Limax maximus, Lin.

Also, New Bedford and Cambridge, Mass., and New Haven, Conn.

Limax flavus, Lin.
agrestis, Lin.

Stenogyra decollata, Lin.

Arion fuscus, Müll.

Also, New Bedford, Mass. (Thomson).

Fruticicola hispida, Lin.

Also, Gay Head, Martha's Vineyard, Mass. (Thomson).

Fruticicola rufescens, Pennant.

Also, Naushon, Buzzard's Bay, Mass. (Thomson).

Fruticicola Cantiana, Montagu.

Plate I. Fig. 13.

Quebec, Canada (F. R. Latchford).

I am indebted to the discoverer for specimens preserved in spirits which furnished the following notes.

Genital system complicated with accessory organs in the form of vaginal prostates, one long, narrow, flagellate, tapering at apex, four short, cylindrical, bluntly terminating. Genital bladder very large, oval, on a narrow duct. Penis sac stout, tapering above into a flagellate extension, at the commencement of which the vas deferens enters.

Jaw low, wide, ends attenuated, blunt: over twelve flat, broad, crowded ribs, whose ends denticulate either margin.

Lingual membrane with 40–1–40 teeth. Centrals tricuspid; laterals bicuspid; marginals also bicuspid without the inner cutting point being bifid.

Turricula terrestris, Chemn.
Tachea hortensis, Müll.

Pomatia aspersa, Müll.

Also, San José, Cal.

Besides the above, that have more or less firmly established themselves here, various species have from time to time been noticed living, but the individual or colony has died out. Some of these are: —

Zonites cultellatus	See Vol. V. p. 135
alliarius	" " 135
Stenogyra octona	" " 196
Bulimulus obscurus	" " 212
Pupa marginata	" " 213
Helix depicta	" " 256
Pisana	" " 256
arbustorum	" " 256
lactea	" " 257
variabilis	" " 257
Bulimus acutus	" " 399
Succinea putris	" " 430
amphibia	" " 430

UNIVERSALLY DISTRIBUTED SPECIES.

For all of these see Vol. V.

Patula striatella, Anthony.
Microphysa pygmæa, Drap.*
Helicodiscus lineatus, Say.
Vallonia pulchella, Müll.
Pupa muscorum, Lin.
Zonites nitidus, Müll.
Zonites arboreus, Say.
indentatus, Say.†
minusculus, Binn.
viridulus, Mke.
milium, Morse.
fulvus, Drap.

* See below, page 35.

† See Supplement I. for *Zonites subrupicola*.

CENTRAL PROVINCE SPECIES.

Macrocyclis Vancouverensis, Lea.

A species of the Pacific Province, confined to the vicinity of the coast range in California. Above Lat. 49° it passes the Cascade Mountains, reduced in size, and ranges southeasterly into Idaho and Montana. I have actually received it from the Cœur d'Alène Mountains, Idaho: Umatilla Co., E. Oregon: Walla Walla, E. Washington Territory.*

Macrocyclis Hemphilli, W. G. Binn.

Weston, Umatilla Co., E. Oregon. A species of the Oregon region.

Limax montanus, Ingersoll.

Also near Salt Lake City, Utah (H. Hemphill).

Zonites Whitneyi, Newcomb.

Also Emigrant Cañon, near Salt Lake City, Utah (Hemphill).

Zonites nitidus, Müll.

Near Santa Fé, New Mexico. A universally distributed species.

Zonites arboreus, Say.

A universally distributed species. Actually found also at Franklin, White Bird Creek, Idaho: White Pine, Austin, Nevada: near Salt Lake City, Provo, Weber Cañon, Utah. (Hemphill.)

Zonites viridulus, Menke.

A universally distributed species. Found also in Utah (Hemphill).

Zonites indentatus, Say.

A universally distributed species.

* It must be borne in mind that changes are constantly being made in the boundaries of the newer States and Territories. I use the names as now accepted, 1886.

Zonites minusculus, Binney.

Universally distributed.

Zonites milium, Morse.

Not actually received from the Central Province, but no doubt existing there, as it has been found over the Eastern and Californian Provinces. Probably a universally distributed species.

Zonites fulvus, Drap.

A universally distributed species, received from numerous localities in Utah, Nevada, and Colorado.

Vitrina Pfeifferi, Newc.

A species of the California Province. I have received it also from Logan Cañon, Weber Cañon, St. George, and Salt Lake City, Utah; Austin and White Pine, Nevada: White Bird Creek, Idaho. (Hemphill.)

Patula solitaria, Say.

Plate I. Fig. 10.

A species of the interior region of the Eastern Province. I have received it also from White Bird Creek, Idaho; Walla Walla, Washington Territory; Weston, Oregon (Hemphill); in addition to the localities given in Vol. V. These last two points are about twenty-five miles apart, at the foot of the Blue Mountains, one hundred and fifty miles from the Dalles.

The specimen figured, which is unusually elevated, is from Salmon River Mountains, Idaho (Hemphill). A uniformly brown specimen with narrow white band was also found.

One of the most unlooked for and interesting facts in the geographical distribution of our land shells is the westward range of *P. solitaria*, reaching through the Central Province into the Pacific Province to within a few miles of the Pacific Ocean. (See extracts from Mr. Hemphill's letter on pp. 27, 28.)

Patula strigosa, Gould.

Plate II.

This is the most variable species found in North America. The original specimen (see Pl. XXVI. *a*), found on or near the Pacific Coast at Puget Sound by the naturalists of the Wilkes Exploring Expedition, is large, almost discoidal, with widely open umbilicus. It could not possibly occur to me that there were any relations between it and the small, globose, narrowly umbilicated, highly

elevated shell which I described from what was then Nebraska as *Helix Cooperi*. (See Vol. IV. Pl. LXXVII. Fig. 11.) Equally confident was Dr. Newcomb that the small, carinated, lenticular shell described by him from Nevada as *Helix Hemphilli* was new to science. Subsequently, Dr. Gabb described as *Helix Haydeni* what appeared to be a distinct species with heavy revolving ribs. More recently authors less acquainted with the group have added to the synonymy by describing under the names of *H. militaris* and *H. Bruneri* what appeared to them to be new species. When the researches of Mr. Hemphill and others had brought large numbers of specimens from many localities in the Central Province, it became evident that what had appeared distinct species were connected by intermediate forms, and therefore should be considered varieties only. Even *Helix Idahoensis* also seemed to be but an aberrant form of the same protean species. Then came the explorations of Mr. Hemphill in Utah, bringing to light several more well-marked varieties, constant in their respective localities, several of which would be recognized by most naturalists as good species. Mr. Hemphill has distributed these as var. *Wasatchensis*, *Oquirrhensis*, *Newcombi*, *Gouldi*, *Binneyi*, *albofasciata*, *castanea*, *Utahensis*, *Gabbiana*, *multicostata*, — names printed in his catalogue, though as yet unaccompanied by descriptions or figures.

I here propose treating separately each of these marked varieties. It must be borne in mind that in each form there is found considerable variation in size, in elevation of spire, and breadth of umbilicus.

The geographical range of the group is very great. Though *Idahoensis*, *Haydeni*, and most of Mr. Hemphill's varieties are restricted to narrow limits, the forms usually referred to *strigosa* and *Cooperi* have been found from the Lake of the Woods to the Rocky Mountains in the British Possessions on the north, to numerous localities in New Mexico and Arizona on the south. The eastern boundary is the main range of the Rocky Mountains, but in Wyoming and Dakota (as now constituted) it is found more easterly, even in the Black Hills at longitude 104° in the southwestern corner of Dakota, the original locality of *Cooperi*. It was not, however, found by Mr. Hemphill at Helena, Montana, nor nearer to it than a point two hundred miles south on the road to Salt Lake City. On the west, it ranges to the Sierra Nevada and Cascade Mountains, and passes the latter even to the Pacific Ocean, though the specimens collected from time to time west of the Cascades in Washington Territory and Oregon may have been individuals brought down by the Columbia River from the regions east of the Cascades, or colonies descended from such. I doubt the species being really an inhabitant of the Pacific Region.

It was Mr. Hemphill who called my attention to this explanation of the presence in the Pacific Province of Central Province species. I cannot do better than quote his words: "I have no evidence of *Patula strigosa* having crossed the summit of the main range of the Sierra Nevada to the westward and entered the Pacific Province. The Cascade range of mountains in Oregon is, as you are aware, a continuation of the Sierra Nevada. It crosses the

Columbia River between the Dalles and Portland, and continues its northerly course on the west side of the Columbia. Numerous spurs, however, break off from the main range, and pass north through East Oregon into Utah and Idaho. One of these spurs, called the Blue Mountains, shoots off the Cascades near Mt. Hood, and runs nearly parallel with the Columbia, forming the eastern boundary of its valley, and is about forty miles from the river, and terminates about abreast of the mouth of Salmon River, Idaho, and on the south side of Snake River. On the north side of Snake River these mountains have local names, but are known by the general name of Bitter Root Mountains. They include Salmon River Mountains, etc. By tracing the course of Snake River and its tributaries you will see it drains the northern part of the great central basin, and when it cut its way through these mountains it very likely drained the great system of lakes that once covered a great part of this central basin. Now the mountain ranges in this portion, northeast, are the metropolis of *strigosa* so far as we know at present; and it is not improbable that many individuals, and quite likely whole colonies, of that species are sometimes carried into the streams by rains and floods, and are borne away on the waters towards the Pacific Coast. Occasionally some of the specimens must find or make a lodgement along the banks of the streams, and if the conditions are favorable a colony will spring up and perhaps spread over the neighborhood. The banks of the Columbia between the Dalles and the mouth of Snake River, a distance of one hundred and fifty miles, are destitute of timber, and are covered for several miles back with loose drifting sand, quite unfavorable to the existence and spread of land shells. The locality where I found the variety *castaneus* was on the bank of the Columbia near Celilo, about fifteen miles above the Dalles, on the east side of the Cascades, but on the west side of the Blue Mountains. This colony must have sprung from specimens brought down the stream by floods. At a subsequent visit it had disappeared. It may be possible some colonies will yet be found on the banks of the river below the Cascades. Very likely the original *strigosa* may have come from some colony planted in this way."

These same remarks will apply to *Patula solitaria*, the group of *Triodopsis Mullani*, and *Mesodon ptychophorus*. In treating each separate form of the species, I propose to follow the suggestion of Mr. Hemphill, as he has had so much better opportunities than any one else to appreciate their variations. He suggests arranging the group, whether considered as varieties or as distinct species, in three series according to the modifications of the sculpture of the shells: A. Shell transversely ribbed. B. Shell smooth or with rough striæ. C. Shell longitudinally ribbed.

A. SHELL TRANSVERSELY RIBBED.

Var. Idahoensis, Newcomb.

Plate II. Fig. 12.

In the comparison of the various forms here given, I call this a variety. I am, however, convinced of its specific weight.

The transverse ribs in this are few, separated, and stout. There are twenty-four upon the body whorl of one individual. It has as yet been found only in Idaho. I give a new figure of a Salmon River Mountain specimen.

Var. Binneyi, Hemphill.

Plate II. Fig. 13.

Box Elder County, Utah (H. Hemphill). (See p. 31.)

This variety has strong rough wrinkles rather than decided ribs, about fifty on the first whorl of one individual. Some individuals have a decided, erect tubercle within the peristome near its junction with the parietal wall of the aperture. There are no revolving bands of color.

This is the first of a remarkable series of varieties or species found by Mr. Henry Hemphill in the region of Great Salt Lake, Utah. I will here give his own description of the habitat of these forms: —

"I commenced collecting at or near Ogden, Utah, and almost the first shell I picked up was the variety I call *Wasatchensis*. (See p. 34.) This pretty and interesting shell I found living among quartzite boulders, in crevices sufficiently large to afford cool and moist retreats during the active summer season, and safe places for hibernating during the cold winter months. This shell seems to be confined in its range to a very limited area, for I did not find a single specimen either dead or living outside of a little plat containing an acre of ground. I have often admired this shell, and think it one of the most interesting varieties I found in Utah, as it combines the characters of *Idahoensis*, *Haydeni*, and *Hemphilli*, as well as of *Cooperi*. Not only on this account is it interesting, but because it is found living on or near the dividing line between the *Idahoensis* group and the *Haydeni* group.* North of Ogden you will see I found all the transverse-ribbed varieties, and south of Ogden all the longitudinal ribbed varieties were found, with the exception of the variety of *strigosa*, just assuming the *Haydeni* sculpturing (near Logan). Not a single transverse-ribbed specimen occurred south of Ogden. Whether this is merely accidental, or whether there are some local causes on either side of this line which influence this change in sculpturing, I cannot say. I only point to the fact, and that it seems a little strange that *Wasatchensis* should be found just on this line.

"In the gulches near Ogden, and also on the mountain slopes among rocks and leaves, I found the typical *strigosa* and *Cooperi*, as well as a number of small shells.

* That is, the transversely ribbed and longitudinally ribbed groups.

"From Ogden I went to Salt Lake City, and thoroughly explored all the cañons, gulches, and other favorable places which I could reach in a day's walk. This only resulted in the finding of the typical *strigosa* and *Cooperi*, both large and small.

"I next went to Provo, Utah, fifty miles south on the same range of mountains, and there also I found only the typical *strigosa* and *Cooperi*, large and small.

"I then returned to Salt Lake City, and crossed the valley to the west, camping on the west side of a range called the Oquirrh Mountains. Here commenced a series of finds that was quite exciting and very interesting to me. At the foot of the mountain my attention was attracted to a pile of detached rock, usually a good place for snails. After a few moments' work among these stones I was rewarded by finding quite a number of specimens of the variety I call *Utahensis*. (See p. 33.) This has the form of *Hemphilli*, but is destitute of the revolving ridges of *Haydeni*. The specimens were all constant in sculpturing, but varied very much in size and somewhat in form. I next went up the side of the mountain a short distance to another pile of stones (limestone), and here I found the variety I call *Oquirrhensis*. (See p. 34.) This has quite prominent revolving ribs, more developed than in the typical *Hemphilli* from White Pine, Nevada. This colony was also constant in sculpturing, but varied very much in size, and also in form. I next went along the mountain side, and crossed a little ravine, and commenced raking among the leaves and brush on the steep slope of the mountain. Here I found a colony of the typical *Haydeni*, constant in sculpturing, but as in the case of the other colonies, variable in size and form. Following up this ravine to near the summit of the mountain, I found a few isolated specimens of *Haydeni* under stones. Near the summit I found two specimens of *Cooperi*. I then returned to the bushes where I found *Haydeni*, and after some further work there passed along the side of the mountain a very short distance to another ravine with low bushes covering its sides. Here among the leaves I found a colony of the variety I call *Gabbiana*. (See p. 34.) This is a coarse, rough *Haydeni*, with the revolving ribs nearly or quite obsolete. This variety also maintained its peculiar sculpturing, but varied again in size and form. Continuing my course along the mountain side, I came to another ravine which I followed up a short distance to a perpendicular precipice about fifty feet high, barring farther progress. At the foot of this limestone wall I found another colony of one of the smaller forms, elevated like *Cooperi*, with the revolving ribs nearly obsolete. Here, then, were five colonies of the same species, apparently, living on the same mountain slope, within a short distance one of the other, each colony maintaining its peculiar sculpturing, but varying in size and form.

"In due time I returned to Salt Lake City, where I remained a few days to prepare my specimens.

"Returning to Ogden, I explored the mountains farther to the north than on my first visit, which resulted in finding the variety I have called *Newcombi*. (See p. 32.) This colony I found living among bushes on the steep sides of a gulch facing the north, a spot of continual shade. The specimens, both banded and plain, were quite numerous; but beyond the space of about fifty yards not an individual could be found either above or below. I also found on a rocky point two or three specimens of *Haydeni*, nearer Ogden, on the north side of the city.

"From Ogden I went to Brigham City, and quite thoroughly explored all that vicinity. Here I found a colony of the small albino *strigosa*, with and without the tooth on the peristome. This colony occupied a pile of rocks at the foot of the mountain, shaded by bushes, dead leaves, and the débris washed down the mountain. I did not find this variety elsewhere, nor was a single

banded specimen found among them. The typical and also albinos of *strigosa* and *Cooperi* occurred in this vicinity.

"I continued my course northward from Brigham City, pitching my tent on the banks of Bear River. The valley here was considerably broken by the mountain spurs, through one of which the river had cut its way, leaving high rocky cliffs on either side, with scattered clumps of bushes along the river and on the edges of the bluffs. Everything seemed favorable here to the existence of snails. My first find was near the edge of the bluff, in cattle tracks and small shady holes in the ground, of the white variety I call *Binneyi*. (See p. 29.) These were all plain white. They were quite plentiful just on the brow of the bluff and the slope towards the river. The next I found was in a clump of bushes among leaves and brush. These I have called variety *albofasciata*. (See p. 32.) The body of the shell is clouded, with the broad, revolving white band at the periphery. Some of this variety are beautifully clouded beneath. None in these bushes were white.

"I next went up to the rocky cliffs about three miles from my camp, and here among bushes I found the plain white varieties, *Binneyi*, with and without the denticle on the peristome. I worked my way among the bushes and rocks to the foot of the cliffs, and here on a mossy, grassy slope, directly at the foot of a high cliff, I found a colony of the ribbed variety *castaneus*. (See p. 32.) This spot is continually shaded by the tall cliff, the sun never shining on it. Most of this colony are faintly marked with the broad white band of *albofasciata*, but a few are plain chestnut-colored. I next crossed a small ravine to another cliff, where a small patch of wild rye was growing very luxuriantly. It was about fifty feet square, directly beneath a little gully in the cliff above, where the melting snows of spring and heavy summer rain formed a little rivulet, pouring over the cliff and irrigating the rye. In this patch I found a very prolific colony of the small interesting variety I have called *Gouldi*. (See p. 32.) So plentiful were they, that I picked up by actual count one thousand in about two hours. No large specimens were associated with them, while the little fellows strayed but a short distance from the rye. No typical *strigosa* were found in this vicinity; all were ribbed.

"From here I went to Logan, Utah, where I found the variety with microscopic revolving ribs, beginning of *Haydeni*, among stones at the head of a gulch quite high on the mountains. The typical *strigosa* and *Cooperi* were found here also.

"I next went to Franklin, just across the Utah line in Idaho, where I found the thin, frail, iron-stained variety of *strigosa*, among red sandstones.

"You will see by this account that nearly all of these colonies were separated, though some of them were but a few yards apart. While the typical *strigosa* and *Cooperi*, large and small, seem to range over the whole region where I collected, Ogden seems to be the dividing line between the transverse-ribbed varieties and the longitudinal-ribbed varieties. No transversely ribbed specimens were found south of Ogden; but a few *Haydeni* and the Logan variety (beginning of *Haydeni*) are all that belong to the *Haydeni* group that I found north of it, excepting a keeled variety found on the mountains of Salmon River, Idaho. Whether there is any meaning in this I cannot say. The field is so large,* many years will be required to work it up thoroughly. I have no doubt other varieties will be found."

* In another of Mr. Hemphill's letters he writes: "The little spot in Utah where I found my Utah series is probably the only one that we may say is worked up in the whole of the great basin of Utah, Nevada, Montana, and Idaho. The field is very large, and there are many ranges of mountains passing through it that must yield some nice things, and no doubt many more varieties of *strigosa* are just waiting for the catcher."

Var. Newcombi, Hemphill.

Plate II. Fig. 8.

Near Ogden, Utah (H. Hemphill). (See *ante*, p. 30.)

This variety has numerous separated, rough, heavy, transverse ribs (forty-four on the first whorl of one individual), and two widely separated, revolving bands of color. It varies, as usual in the group, in size and globoseness. Some want the revolving band.

Var. multicostata, Hemphill

Plate II. Fig. 6.

Box Elder County, Utah (H. Hemphill).

On one specimen I counted over seventy coarse rib-like striæ to the first whorl. There are two revolving bands of chestnut on all the individuals received from Mr. Hemphill. Two have the denticle on the peristome.

Var. Gouldi, Hemphill.

Plate II. Figs. 5, 16.

Banks of Bear River, north of Brigham City, Utah (H. Hemphill). (See p. 31.)

One individual has sixty-two rough wrinkles on the first whorl. There are two revolving bands of color. The specimen figured (Fig. 16) is the largest sent me by Mr. Hemphill, others being smaller by one half, and some being very much depressed (Fig. 5). Among the thousand specimens collected, none were large.

Var. albofasciata, Hemphill.

Plate II. Figs. 3, 4.

Same vicinity as the last. (See p. 31.)

The body of the whorl is clouded, with a broad, revolving white band at the periphery, and white around the umbilicus. Some individuals are white with two revolving bands of color. On one there are about seventy rough wrinkles to the first whorl. Some have a toothlike process on the peristome (Fig. 4). The variety differs, as usual in the group, in the elevation of the spire and in size.

Var. castaneus, Hemphill.

Plate II. Figs. 11, 14.

Box Elder County, Utah (see p. 31): also Celilo, 15 miles from the Dalles, Oregon.* (Hemphill.)

* Probably a colony brought down by the Columbia. It was not found on a subsequent visit.

This variety differs somewhat in the sculpturing. The wrinkles are usually less developed than in the previously mentioned varieties, but on a few individuals are coarser. Those from Eastern Oregon are almost smooth. The principal characteristic of the variety is its color, which is uniform chestnut, excepting around the umbilicus. A few like the one figured have a double revolving white band.

This closes the series of transversely ribbed varieties.

B. SHELL SMOOTH OR STRIATE.

In this section Mr. Hemphill suggests including the typical *strigosa* (see Pl. XXVI.[a]), a large, flattened, widely umbilicated, almost discoidal form, and the typical *Cooperi* (Vol. IV. Pl. LXXVII. Fig. 11), a small, elevated, globose, narrowly umbilicated shell, as well as the innumerable varieties of size and form and coloring which exist, some of which I have figured in Vol. IV. In none of these variable forms do we find either transverse or revolving ribs.

Some individuals are of a dirty white, but usually two revolving chestnut bands are present: others, retaining the bands, are mottled with light or dark horn-color, or more or less completely banded or uniformly colored with light or dark chestnut. Within the peristome on some is a decided denticle, such as I have already described above for other varieties of the group. (Pl. II. Fig. 4.)

One colony from Eastern Oregon is peculiar in form. (Pl. II. Fig. 10.)

This restricted form of *strigosa*, including *Cooperi*, is found over all the wide region indicated for the species on p. 27. The Arizona localities from which I have received it are Logan, near Phœnix: Pine Creek, below Natural Bridge: Huachuca Mountains.

Var. Utahensis, Hemphill.

For locality, see *ante*, p. 30. This is a rough, coarse, carinated *strigosa*, figured in Terr. Moll., V. p. 158, Fig. 66. The peristome is sometimes continuous by a heavy raised callus connecting its terminations. It is sometimes smaller and more elevated.

C. SHELL LONGITUDINALLY RIBBED.

Var. Hemphilli, Newcomb.

Plate II. Fig. 15.

This form seems widely distributed. It was originally found by Mr. Hemphill at White Pine, Hamilton, Nevada. Mr. Hemphill believes it will be found all through the mountains bordering on both sides of the Snake River Valley, Salmon River Mountains, Idaho. He also found it at various points in Utah

and Colorado. The original specimen figured in Vol. V. being immature, I here give (Pl. II. Fig. 15) one of a mature individual. Above (p. 31), are noticed specimens from Logan, Utah, showing the gradual change from *strigosa* to *Hemphilli*.

The variety *Hemphilli* is characterized by minute revolving striæ, and is decidedly carinated.

Var. Oquirrhensis, Hemphill.

Plate II. Fig. 12.

Oquirrh Mountains, Utah (H. Hemphill). (See p. 30.)

This form has quite prominent, revolving ribs, more developed than in the typical *Haydeni*. The aperture is oblique, the ends of the peristome approached and joined by a heavy callus. There is a strongly developed carina. Albino individuals were found.

H. Bruneri, Ancey, is a synonym of *Oquirrhensis*.

Var. Gabbiana, Hemphill.

Plate II. Fig. 9.

Near Salt Lake City (H. Hemphill). (See p. 30.)

As described by Mr. Hemphill above, this variety is a coarse, rough *Haydeni*, with the revolving ribs nearly or quite obsolete. Like all the other varieties, it varies in size and shape. The ends of the peristome are nearly approached, and often continuous.

Var. Haydeni, Gabb.

Utah (H. Hemphill). (See p. 30.)

This well-known form has the revolving ribs most developed of all. For figure see Terr. Moll., V. p. 159.

Var. Wasatchensis, Hemphill.

Plate II. Fig. 7.

Wasatch Mountains, Utah (H. Hemphill). (See p. 29.)

This is the most peculiar variety, with coarse revolving striæ and ribs (sometimes wanting), rough transverse wrinkles, decided carina crenellating the sutures, ends of peristome approached: the umbilicus is very narrow: the shell is elevated, often pyramidal: apex acute. Albino individuals were also found. With its peculiar pyramidal spire and small umbilicus it combines the sculpturing peculiar to several of the other varieties. (See p. 29.)

Patula striatella, Anthony.

This species, including *Cronkhitei*, has also been found in Wyoming and at Ogden Cañon, Utah: Nevada: Colorado. (Hemphill.)

Patula Horni, Gabb.

Also Logan, Arizona.

Microphysa Ingersolli, Bland.

Plate III. Fig. 5.

A better figure than that in Vol. V. is here given.

Also found by Mr. Hemphill at Weston, Umatilla Co., Oregon: Mount Nebo, Wasatch Mountains, Logan Cañon, Utah. Also found by Mr. Ernest Ingersoll near Lawrence, Kansas, on the banks of the Kaw.

Microphysa pygmæa, Drap.

Admitted as a universally distributed species (see p. 24), though not actually as yet received from the Central Province. Sharing the peculiarity of jaw with all our species of *Microphysa*, I have placed it in that genus.

Microphysa conspecta, Bland.

Plate III. Figs. 4, 6.

Living specimens received from Dr. J. G. Cooper have enabled me to ascertain that this species has the jaw characteristic of *Microphysa*. My figure, drawn by camera lucida, gives the sixteen plates as they became actually disarranged under pressure, showing them to be separated and not forming one solid piece as in most of the genera. The central plates are not imbricated, and appear lightly connected. The other plates appear to overlap laterally on their outer sides. The jaw is low, wide, slightly arched, the ends scarcely attenuated, blunt.

There are 12–1–12 teeth on the lingual membrane. Centrals with long and narrow base of attachment: reflection small, with three cusps, the middle one much the largest, all bearing short cutting points. Laterals same, but bicuspid. Marginals low, wide, with two broad cusps, each bearing a broad, bifid cutting point. The centrals and laterals are quite like those of *Pupa*.

A species of the Pacific Province also.

Helicodiscus lineatus, Say.

A universally distributed species, found over the Central Province, as stated in Vol. V. Specimens collected at Oakland, California, and in Idaho by Mr. Hemphill, quite want the revolving lines.

Polygyrella polygyrella, Bland.

Plate I. Figs. 6, 7; Plate VI. Fig. 8.

Also in Deer Lodge Valley, Montana (Hemphill).

The genital system (Pl. III. Fig. 8), as would be anticipated, is characterized by the length of all the organs. The penis sac (*p. s.*) is long, narrow, cylindrical, receiving the vas deferens at its blunt apex, and bearing the retractor muscle just below. The genital bladder (*g. b.*) is long, narrow, pointed above and below; its duct is long and narrow. The testicle and ovary are long and narrow.

Triodopsis Levettei, Bland.

Plate I. Fig. 15.

See Supplement to Vol. V. p. 154.

Also seventy miles southeast of Tucson, in the Huachuca Mountains, Arizona. A species of the Central Province rather than of the Texas Region, as suggested in "Manual of American Land Shells."

Triodopsis Mullani, Bland

I am convinced by larger suites of specimens that I was wrong in referring (Vol. V. p. 333) this species to *Mesodon devius*. The group is very puzzling, and some confusion has resulted from my treatment of it. It must, therefore, be considered that *Triodopsis Mullani*, Bland, as described and figured by him is a distinct species confined to the regions east of the Cascades in Northern Idaho. It is very globose, with a decidedly tridentate aperture. (See Vol. V. p. 338, Fig. 222, and Man. Amer. Land Shells, p. 119, Fig. 87, for a copy of Bland's original description.) The shell I describe below as *T. Sanburni* is somewhat nearly related to *Mullani*, but has its aperture much more contracted by the teeth on the peristome and the more developed parietal tooth. *T. Harfordiana* is the form which in Terr. Moll., V. (309, Fig. 203) I mistook for *Polygyra Harfordiana* (see Suppl. p. 151). It is a small shining shell, flattened, with larger umbilicus and less developed teeth. *Triodopsis Hemphilli* is a much larger, coarser, russet-colored shell, scarcely umbilicated, with a small parietal tooth, and a slight approach only to the lamellar dilatation of the inner edge of the peristome so characteristic of the typical *devius;* no denticle on the outer edge of the peristome. All these forms show the scars on the epidermis, though no hairs were present in my fresh specimens. Besides these well-marked forms are found individuals, not associating with them, which seem to connect *Harfordiana* with *Mullani* (see Terr. Moll., V. Fig. 221, and the following, Pl. I. Figs. 6, 7). The typical *Mesodon devius* is confined to the Pacific Province. See Terr. Moll., IV. Pl. LXXIX. Fig. 13; V. Fig. 220. It is a very distinct species, as yet not noticed in the Central Province.

Triodopsis Sanburni.

Plate I. Fig. 9; Plate III. Fig. 3.

Shell narrowly umbilicated, globose, depressed, thin, sparsely hirsute, with distant, scarcely perceptible wrinkles of growth, yellowish horn-colored; whorls five and one half, slightly convex, the last hardly descending, beneath convex; aperture oblique, lunate, trilobed, with a heavy, prominent, blunt parietal tooth; peristome white, broad, reflected, almost covering the umbilicus, thickened, bearing on its right margin a large squarely truncated denticle, on its basal margin a stout, bluntly pointed denticle, the two denticles separated by a small, rounded sinus. Greater diameter, 11 mm.; lesser, 10 mm.; height, 5 mm.

Kingston, Northern Idaho (J. Rand Sanburn).

Lingual membrane as usual in the genus. Teeth 26–1–26, with about eight laterals on either side, the ninth tooth having its cutting point split, the eleventh in another membrane: centrals with slightly developed side cusps and decided cutting points: laterals like the centrals, but bicuspid: marginals long, low, with two very wide, blunt cusps, the inner much the larger, both bearing long, oblique, irregularly bifid or trifid cutting points. (Pl. III. Fig. 3.)

Genital system with no accessory organs. Penis sac long, cylindrical, somewhat attenuated at its apex, where it receives the vas deferens and retractor muscle: genital bladder long, narrow, suboval: duct to genital bladder stout below, gradually tapering above. The same arrangement is found in the genitalia of the typical *devius*.

This shell, found in quantities living by Mr. Sanburn, shows no variation excepting slightly in size. There are no individuals showing a transition to forms of *Mullani*. It is nearly allied to that species as described by Mr. Bland. It is, however, much less globose, and has its aperture very much more contracted by teeth. The parietal tooth is not long and curving, but erect and of equal width to its bluntly truncated top. The upper tooth on the peristome, opposite, not above, the parietal tooth, is also erect and bluntly truncated. The lower peristome tooth is bluntly triangular. The sinus between the two parietal teeth is small and rounded.

I have described the shell as hirsute, though no hairs were found on the scars which surely bore them.

The general appearance of the shell is that of *T. Hopetonensis*.

Triodopsis Harfordiana.

Plate I. Figs. 6, 7.

Shell umbilicated, depressed, thin, shining, sparsely hirsute, greenish horn-colored, wrinkles of growth not prominent; whorls four and a half, hardly convex, the last scarcely descending, deeply grooved behind the peristome, hardly convex beneath; aperture very oblique, lunate, trilobed, with a small

parietal tooth; peristome narrow, scarcely reflected, bearing two distant, slightly developed denticles. Greater diameter, 8½ mm.; lesser, 8 mm.; height, 3 mm.

Triodopsis Harfordiana, W. G. Binney, not of J. G. Cooper, Terr. Moll., V. 309, figure only, not description: Pl. VIII. Fig. R, lingual dentition.
Mesodon devius, var., W. G. Binn., Man. Amer. Land Shells, 118, Fig. 88.

Salmon River, Idaho (H. Hemphill).

Genitalia unobserved.

Lingual dentition (under erroneous name of *Triodopsis Harfordiana*). See Terr. Moll., V. l. c.

This is the shell formerly mistaken by me for *Polygyra Harfordiana*. It is a small, very much depressed, shining shell, with open umbilicus and slightly developed teeth. Its surface is scarred as if it had been hirsute. Though much more depressed, it has the general appearance of a tiny *T. tridentata*.

Triodopsis Hemphilli.

Plate I. Fig. 17.

Shell imperforate, globosely depressed, coarse, slightly wrinkled, russet-colored, sparsely hirsute; whorls five and a half, convex, the last globose, slightly descending; aperture very oblique, lunate, with a short, narrow, slightly curving parietal tooth; peristome white, broad, thickened, revolute, usually quite concealing the umbilicus, bearing on its basal margin an elongated, lamellar toothlike process. Greater diameter, 17 mm.; lesser, 14 mm.; height, 7 mm.

Kingston, Northern Idaho (J. Rand Sanburn).

The surface is scarred as if hirsute when quite fresh.

The shell, by its coarser texture, closed umbilicus, and lamellar peristome denticle, is more nearly allied to the typical *Mesodon devius* than to *Mullani*, *Harfordiana*, or *Sanburni*. Though common at the locality given above, it is not variable, nor have I received it from other points.

Lingual membrane of the same character as in *T. Sanburni*.

Genitalia as in the last-named species.

Mesodon ptychophorus, A. D. Brown.

Plate I. Figs. 3, 16.

Shell with umbilicus almost concealed, globose, with coarse, distant striæ of growth, thick, of a dull russet-color; spire elevated, apex acute; whorls five, convex, the last swollen below, rapidly descending; aperture oblique, subcircular, parietal wall with light callus; peristome white, thick, narrow, reflected, with a thickening scarcely approaching a tooth-like process on its basal margin, its

termination almost entirely concealing the small umbilicus. Greater diameter, 19 mm.; lesser, 15 mm.; height, 11 mm.

Var. MAJOR. Six full whorls, umbilicus less concealed. Greater diameter, 22 mm. (Fig. 3.)

Helix ptychophora, A. D. BROWN. See Vol. V. p. 355.
Arionta Townsendiana, var., W. G. BINN. l. c. Suppl., Pl. IV. Figs. E, F. — Man. Amer. Land Shells, p. 128, Figs. 101, 102.

Deer Lodge Valley, Montana: the large variety was found by Mr. Hemphill along Salmon River, Idaho: Bitter Root Mountains, Umatilla Co., Oregon: Weston, Oregon, to the Dalles. The range westwardly through the Cascades has been already explained above (see p. 28).

Formerly I was disposed to believe this to be a variety of *Arionta Townsendiana*, but the larger number of specimens received from various localities has convinced me of its being distinct. It is a true *Mesodon*, very much like *M. clausus*. It is a smaller shell than *Townsendiana*, more globose, less widely umbilicated, with more circular aperture; the sculpturing lacks the transverse striæ and malleations of the *Ariontæ*.

For genitalia, jaw, and lingual dentition, see Terr. Moll., V.

To my knowledge, *Arionta Townsendiana* has not been found east of the Cascade Mountains.

Mesodon Columbianus, LEA.

Plate I. Fig. 5.

A species of the Pacific Province as well as the Central Province. Also received from Cœur d'Alène Mountains, Idaho: Deer Lodge Valley, Montana. (H. Hemphill.)

One Cœur d'Alène Mountain specimen with parietal tooth is figured.

The form found at these Central Province localities is the variety called *labiosa* by Gould. It is more globose than the type, has a more circular aperture, without the horizontal basal margin or toothlike thickening to the peristome. The latter is extremely broad, grooved, not flattened. It must be remembered that this toothed form is not the *armigerus*, Ancey, which will be treated under the Pacific Province species.

Vallonia pulchella, MÜLL.

A universally distributed species. Also at various points in Utah (Hemphill).

Pupa muscorum, LIN.

Plate III. Fig. 11.

Universally distributed.

The shell figured, which appears to me identical with this species, was sent to me by Mr. Ancey as *P. sublubrica*, from White Pine, Nevada.

Pupa Blandi, Morse.

A northern region of Eastern Province species. Also found at Ogden and in the Wasatch Mountains, Utah (Hemphill).

Pupa corpulenta, Morse.

Ogden Cañon, Utah, with two parietal teeth (Hemphill).

Pupa Arizonensis, Gabb.

Plate III. Fig. 10.

I give a figure of *Pupa hebes*, Ancey, drawn from a specimen sent me by Mr. Ancey. To me it seems identical with *Arizonensis*.

Pupa hordeacea, Gabb.

Pupa alticola, Ingersoll.

Plate III. Fig. 9

A better figure of an authentic specimen is given here. Wasatch Mountains, Utah (Hemphill): Ouray, Colorado (Ingersoll).

Vertigo ovata, Say.

A universally distributed species.

Ferussacia subcylindrica, Lin.

Also from various points of Utah, Idaho, and Nevada.
A species also of the northern region of Eastern Province.

Succinea Haydeni, W. G. Binn.

Also, Salt Lake City, Utah. A species of northern region.

Succinea Sillimani, Bland.

Succinea lineata, W. G. Binn.

Also in Idaho. A northern region species. As *S. chrysis* it is also described from Alaska. (See Man. Amer. Land Shells, p. 473, Fig. 515; and below, p. 46.)

Succinea Stretchiana, Bland.

Also at Elko, Nevada

Succinea avara, Say.

A northern region species. (See Vol. V. p. 420.)

PACIFIC PROVINCE SPECIES.

I have not included the species from the extreme northern regions, which more properly belong to the fauna of Asia. Such are: —

Pupa arctica Wall.
columella, Benson.
Succinea turgida, West.
annexa, West.
Vallonia asiatica, Nevill.
Pupa edentula, Drap.
signata.
muscorum, var. **Lundstromi.**
columella, var. **Gredleri.**
Krausseana, Reinh.

See Man. Amer. Land Shells, pp. 473, 474.

Macrocyclis Vancouverensis, Lea.

A dark reddish variety was found in Alaska by Mr. Dall.

Macrocyclis sportella, Gld.

Macrocyclis Voyana, Newc.

A variety *simplicilabris* has been noticed by Ancey (Le Naturaliste, IV. pp. 110, 111).

Macrocyclis Hemphilli, W. G. B.

See also p. 25. Found also at Freeport, W. Terr.

Macrocyclis Duranti, Newc.

Haplotrema has been suggested as a subgeneric name for this species (Ancey, l. c.) on account of its simple peristome.

Zonites Whitneyi, Newc.

See also p. 25.

Zonites nitidus, Müll.
Zonites arboreus, Say.
Zonites cellarius, Müll.

See p. 23.

Zonites indentatus, Say.
Zonites viridulus, Mke.

Portland, Oregon (Hemphill) : Victoria, British Columbia (Rev. G. W. Taylor).

Zonites milium, Morse.
Zonites chersinellus, Dall.

See Supplement I.

Zonites fulvus, Müll.
Vitrina Pfeifferi, Newc.

See page 26.

Limax campestris, Binn.
Limax Hewstoni, J. G. Coop.
Limax hyperboreus, Westerlund.

See Man. Amer. Land Shells, p. 473.

A species collected in Arctic America by the "Vega." I am indebted to Mr. Dall for a specimen from Commander Island, Siberia.

Jaw arched, smooth, with median projection. Lingual membrane with about 42–1–42 teeth. Centrals tricuspid : laterals bicuspid, twelve in number on each side: marginals about thirty in number on both sides, aculeate, simple, without bifurcation or side spur. Fig. 516 of Man. Amer. Land Shells shows a central tooth with its adjacent lateral and three extreme marginals of Mr. Dall's specimen.

From Seattle, Washington Territory, I have received a small *Limax* similar in outward appearance to *hyperboreus*, and with similar dentition.

See Westerlund, Sibirien Land och Sötvatten Mollusker, p. 21.

Prophysaon Hemphilli, Bl. & Binn.

Prophysaon Andersoni, J. G. C.

It is a true *Prophysaon*, though described originally as an *Arion*.

The lingual membrane has 30–1–30 teeth, with about 12 perfect laterals. Centrals tricuspid : laterals bicuspid : marginals with one long, stout, oblique inner cutting point, and one outer, short, blunt, sometimes bifid cutting point. Resembling that of *P. Hemphilli*.

Jaw low, arcuate, ends blunt; with numerous (over 15) irregularly developed, broad, stout ribs, denticulating either margin.

Animal small, long, and slender, dirty white with dark reticulations: an indistinct dark-colored circle around the mantle near its edge, and a dark band running longitudinally from the rear of the mantle to the tail on each side of the centre of the back.

Reticulations foliated as in *Prophysaon Hemphilli* and in the figure of *Arion foliolatus*. The mantle covered with minute tubercles, not foliated.

The animal extends itself into a long cylindrical worm-like body, with obtuse ends. Length when fully extended, 60 mm.

The synonymy of this species is as follows: —

Arion Andersoni, J. G. Coop., formerly *Prophysaon Hemphilli*, var., W. G. B., T. M. V.

Prophysaon Andersoni, J. G. C., in letters.

Ariolimax Columbianus, Gould.
Ariolimax Californicus, J. G. Coop.
Ariolimax niger, J. G. Coop.
Ariolimax Hemphilli, W. G. B.

Ariolimax Andersoni, W. G. B.

Formerly I supposed this species to be *Arion Andersoni*, of Dr. Cooper. Learning that Dr. Cooper's species is a *Prophysaon*, I still retain for this the specific name *Andersoni*, W. G. B.

Arion foliolatus, Gld.

Still a doubtful species, known only by the original figure and description.

Binneya notabilis, J. G. Coop.

Also found by Mr. Orcutt fifty miles from St. Quentin Bay, Lower California.

Hemphillia glandulosa, Bl. & Binn.

Patula striatella, Anth.

Mariposa, California.

Patula pauper, Mor.
Patula asteriscus, Morse.

Tacoma, W. Territory.

Patula solitaria, Say.

Plate I. Fig. 10.

This can hardly be considered a species of the Pacific Province, though colonies have been found west of the Cascades. (See pp. 27, 28.)

The specimen figured was found by Mr. Hemphill at White Bird Creek, Salmon River, Idaho.

Microphysa Lansingi, Bland.
Microphysa pygmæa, Drap.

See p. 35.

Microphysa conspecta, Bl.

See p. 35.

Microphysa Stearnsi, Bl.

See Supplement I. p. 147. Found also in Alaska.

Helicodiscus lineatus, Say.
Vallonia pulchella, Müll.

San Diego, California.

Gonostoma Yatesi, J. G. Coop.
Polygyra Harfordiana, J. G. Coop
Triodopsis loricata, Gld.
Stenotrema germanum, Gld.

Mesodon Columbianus, Lea.

The true *M. Columbianus* is correctly described and figured in Terr. Moll,. II. and III. It is very readily distinguished by its peristome, the basal margin of which is horizontal in its direction, with a slight thickening or projection before it reaches the base of the shell. It does not appear to range as far southerly as California. Northerly it has been found to 59° latitude.

The form called *labiosa* by Dr. Gould (see Vol. II.) is recognized by its very circular aperture, its widely reflected, sinuous peristome, sharp on its outer edge, not flattened on its face. Its upper surface is elevated as in *Columbianus*. It is sometimes toothed. Originally found in the region of Astoria, Mr. Hemphill has collected it at Kalama on the Columbia River, forty miles below Portland, and also from Deer Lodge Valley, Montana, and in the Cœur d'Alène Mountains, Idaho. (See p. 39.)

My Figs. 4, 5 of Plate I. show the toothed variety from Idaho and an enlarged view of the epidermis. It is less hirsute than *armigerus*.

The form called *armigerus* by Ancey (Le Naturaliste) is the one common in California, ranging as far south as 37° 20′. I have figured it on Pl. I. Fig. 12, as well as an enlarged view of the epidermis. It is the most densely hirsute of the group. It is a more globose shell below than the typical form. The peristome is narrow, much less developed; the parietal tooth is long and narrow, sometimes wanting. It has much the appearance below of a large *Stenotrema germanum*, with which species I have confounded it rather than with *Columbianus*. I have no doubt it will eventually be considered a distinct species.

Mesodon devius, Gld.

As restricted (see p. 36), this species seems to be confined to the Oregon region.

Aglaja fidelis, Gray.
infumata Gld.
Aglaja Hillebrandi, Newc.
Arionta arrosa, Gld.

Arionta Townsendiana, Lea.

As restricted (see p. 39), this species seems confined to the Oregon region.

Arionta exarata, Pfr.

Arionta Californiensis, Lea.

As proposed in Man. Amer. Land Shells, I unite under this specific name the various forms described as—

Helix vincta, Val. (See Vol. IV. for a facsimile of figure.)
Nickliniana, Lea. (See Vol. III. Pl. VI. Fig. *a*.)
arboretorum, Val. (See Vol. IV. Pl. LXXXVI. Fig. 13.)
nemoraviga, Val. (See same, Pl. LXXIX. Fig. 11.)
anachoreta, W. G. B. (See same, Pl. LXXVI. Fig. 5.)
ramentosa, Gld. (See Vol. V.)
Parkeri, Tryon.
reticulata, Pfr. (See Vol. V.)
Bridgesi, Newc. (See Vol. V.)

I have figured, in Man. Amer. Land Shells, Fig. 109, a large umbilicated form, probably very near to Newcomb's type of *H. Bridgesi*, a small umbilicated form (Fig. 168), a larger imperforate form (Fig. 111), and a figure of a shell received under the name of *Diabloensis* from Dr. Cooper (Fig. 113).

Arionta intercisa, W. G. Binn.

I am now convinced that *redimita* is a variety of this species.

Arionta Ayersiana, Newc.
tudiculata, Binn.
Mormonum, Pfr.
Arionta Traski, Newc.
Carpenteri, Newc.
Dupetithouarsi, Desh.

Arionta sequoicola, J. G. C.

An enlarged view of the sculpturing of this species is given in Man. Amer. Land Shells (Fig. 127)

Arionta ruficincta, Newc.
Gabbi, Newc.
Arionta Kelletti, Forbes.
Stearnsiana, Gabb.

Euparypha Tryoni, Newc.

The allied species *E. levis*, Pfr., recently collected by Mr. Orcutt in Lower California, has a genital system (Pl. III. Fig. 2) very near that of *E. Tryoni* (see Vol. V. Pl. XIV. Fig. *c*). I did not detect the organ 2 in *levis*. The

jaw is high, arched, with blunt ends: six ribs on the anterior surface, denticulating either margin. The lingual membrane (Pl. III. Fig. 1) is long and narrow: teeth 38–1–38, with about nine laterals on either side, the tenth tooth having the inner cutting point bifid: centrals and first laterals without side cusps and cutting points: marginals low, wide, with two distinct cusps, each furnished with bifid cutting points.

Pomatia aspersa, Müll.

See p. 24.

Glyptostoma Newberryanum, W. G. B.

Ferussacia subcylindrica, Lin.

Received also from Washington Territory.

Pupa Rowelli, Newc. **Pupa Californica**, Newc.

Pupa muscorum, Lin.

A variety *Lundstromi*, Westerlund, has been described from Alaska.

Succinea Sillimani, Bl. **Succinea rusticana**, Gld.
Stretchiana, Bl. **Nuttalliana**, Lea.
Hawkinsi, Baird.

Succinea chrysis, Westerlund.

Alaska. This is the well-known yellowish variety of *S. lineata*, often found at far northern points. An authentic specimen is figured on p. 473 of Man. Amer. Land Shells.

Succinea Oregonensis, Lea.

Succinea avara, Say.

Received also from California.

Veronicella olivacea, Stearns.
Onchidella borealis, Dall.
Onchidella Carpenteri, W. G. B.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. Mesodon armigerus.
" 2. Same : epidermis enlarged.
" 3. Mesodon ptychophorus, *var.* major.
" 4. Mesodon labiosus.
" 5. Same : epidermis enlarged.
" 6, 7. Triodopsis Harfordiana.
" 8. Mesodon armigerus.
" 9. Triodopsis Sanburni.
" 10. Patula solitaria.
" 11. Triodopsis Mullani.
" 12. Polygyrella polygyrella.
" 13. Fruticicola Cantiana.
" 14. Polygyrella polygyrella.
" 15. Triodopsis Levettei.
" 16. Mesodon ptychophorus.
" 17. Triodopsis Hemphilli.

PLATE II.

Fig. 1, 2. Patula Idahoensis.
" 3. Patula strigosa, *var.* albofasciata.
" 4. Patula strigosa, *var.* albofasciata : toothed.
" 5. Patula strigosa, *var.* Gouldi.
" 6. Patula strigosa, *var.* multicostata.
" 7. Patula strigosa, *var.* Wasatchensis.
" 8. Patula strigosa, *var.* Newcombi.
" 9. Patula strigosa, *var.* Gabbiana.
" 10. Patula strigosa, *var.*
" 11. Patula strigosa, *var.* castanea.
" 12. Patula strigosa, *var.* Oquirrhensis.
" 13. Patula strigosa, *var.* Binneyi.
" 14. Patula strigosa, *var.* castanea.
" 15. Patula strigosa, *var.* Hemphilli.
" 16. Patula strigosa, *var.* Gouldi.

PLATE III.

Fig. 1. Lingual dentition of Euparypha levis.
" 2. Genital system of same.
a. genital bladder.
b. penis sac.
c. vas deferens.
d. vaginal prostate.
Fig. 3. Lingual dentition of Triodopsis Sanburni.
" 4 Jaw of Microphysa conspecta.
" 5. Microphysa Ingersolli.
" 6. Lingual membrane of Microphysa conspecta.
" 7. Same of Fruticicola Cantiana.
" 8. Genital system of Polygyrella polygyrella.
a. genital bladder.
b. penis sac.
c. vas deferens.
d. retractor muscle.
Fig. 9. Pupa alticola.
" 10. Pupa Arizonensis.
" 11. Pupa sublubrica.
" 12. Pupa hebes.

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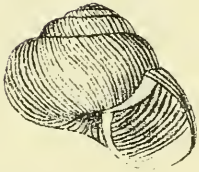
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No. 3. — *Simple Eyes in Arthropods.* *By* E. L. Mark.*

That portion of Mr. Locy's paper on the development of the spider† which deals with the formation of the eye appears to possess importance outside the objects of his special study. The discussion of the bearings of his discoveries on the simple or monomeniscous eyes of Arthropods in general, is the object of the present paper.

Two irreconcilable views have been held of late with regard to the *origin of the retina* in the simple eyes of Arthropods. The writers upon the subject have been pretty evenly divided in opinion. Grenacher, Lankester and Bourne, and Carrière have all claimed, more or less distinctly, that the retina was derived from the "hypodermis;" while Graber, Lowne, and Schimkewitsch have clearly inclined to the opinion that it was an outgrowth from the cephalic ganglia. It has been impossible for either party to establish its views beyond debate, on account of the absence of the proper embryological information.

Grenacher ('79, p. 158) claims the ectodermic (hypodermal) origin of the retina as duly established for certain cases, but admits that, although highly probable, a similar origin has not been proved for eyes of the type to which those of the spiders belong. He says: "Der zweite Punkt auf den es wesentlich ankommt, betrifft die *Herkunft* des Retinaelementes. Was diese anbelangt, so haben wir auch einige Beispiele kennen gelernt, die uns in einer Weise, wie kaum etwas zu wünschen übrig lässt, diese Abstammung klarlegen; nur schade, dass sich so wenige andere anfügen lassen. Mit den ersteren meine ich die Augen der Schwimmkäferlarven (Figg. 1–10, Taf. I), die uns so evident als möglich nicht nur die Abhängigkeit des Retinaelementes, sondern auch aller übrigen Augentheile von dem Integument, der Hypodermis mit Cuticula, erkennen lassen. Damit ist aber für diese Thiere auch zugleich die Abstammung des Retinaelementes vom ersten, äusseren embryonalen Keimblatt, dem Ectoderm, gegeben.

"Nicht so günstig steht es mit den übrigen Formen von Larvenaugen, sowie den einfachen Augen der Spinnen und Insectenimagines. Wenn

* Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College. No. XI.

† Wm. A. Locy, Observations on the Development of *Agelena nævia*, Bull. Mus. Comp. Zoöl., Vol. XII, No. 3, pp. 63–103, 12 pl., Jan., 1886.

auch über die Herkunft *einzelner* Augentheile, über die Abstammung derselben von der Hypodermis, namentlich bei den erstgenannten beiden Catagorien, kein Zweifel obwalten kann, so ist doch hier die Retina in den von mir untersuchten Zuständen ausser aller Continuität mit ihr und jenen Augentheilen, und der erforderliche strenge Nachweis dieses jedenfalls höchst wahrscheinlichen ursprünglichen Zusammenhanges ist erst noch zu führen."

In his last paper on this subject Grenacher ('80, p. 430) reiterates his inability to solve the problem, when he says: "The genesis of the two-layer 'Stemma' out of the hypodermis, to which the conclusions from analogy point, is still entirely obscure to me also, and is only to be made out by direct observation."

Lankester and Bourne ('83) have expressed their opinion on the origin of the retina either in an incidental way or with a certain amount of reserve. I have not hesitated to class them on this side of the question, however, since they evidently incline in this direction. Of the *lateral* eyes in scorpions they say (p. 182): "Both nerve-end cells and indifferent cells of the lateral *ommateum* * apparently belong to the epiblastic layer, and are shut off together with the layer of hypodermis cells from the subjacent connective tissue by a well-marked 'basement membrane,' which in the region of the ommateum may be called the eye-capsule, or, better, the 'ommateal capsule.'" In this connection it should be borne in mind that these *lateral* eyes are claimed by them to be *mono*stichous.† They believe (p. 211), however, that "a few examples clearly transitional between the monostichous and the diplostichous condition have been described by Grenacher (among Myriapods)." Therefore by inference their supposed diplostichous (in reality triplostichous) condition must likewise have had both its layers derived from the hypodermis. The difficulties in the way of this transition from monostichous to so-called diplostichous eyes do not seem to have impressed themselves so forcibly upon these observers as they did upon Grenacher, who, notwithstanding his familiarity with the facts, confessed, as we have seen, that the double-layer condition presented a still unsolved problem.

Finally, they have expressed ‡ more precisely, although incidentally, the conviction that the retina in the *central* ("diplostichous") eyes of the scorpions is of hypodermic origin; but they have nowhere offered an

* "All the soft tissues of an arthropod eye, as distinguished from the cuticular lens," they call "ommateum."

† "An ommateum consisting of a single layer of cells."

‡ See pp. 56, 57.

explanation of the *method* of its formation other than that implied in the allusion to Grenacher's researches on Myriapoda.

Carrière ('85, p. 178), basing his conclusions principally upon the appearances presented by the 'stemma' in the pupa of an ant, believes that it is derived from the hypodermis by, — first, a lenticular thickening of the hypodermis produced by an elongation of the hypodermis cells; and, secondly, by the rearrangement of the latter into two layers, one above the other, of which the outer remains in continuity with the permanent hypodermis and constitutes the "vitreous body," while the inner is transformed into the retina. The *method* by which this rearrangement is accomplished is to be learned a little farther on (p. 189), where he says: "According to my interpretation, therefore, the simple eye (Napfauge) and the compound eye (Fächerauge) of the Arthropoda are organs which arise out of like components in a similar manner (through splitting of the hypodermis into two layers), but in their further development diverge from each other in two opposite directions."

While the authors just quoted agree in believing the retina to be an immediate derivative from the hypodermis, those cited below are at least so far in agreement as to hold that the retina is *not* developed directly from that layer.

Graber's objection to the view that the retina is derived from the hypodermis was based principally upon its total separation from the hypodermis and its derivatives (pigment-cells and "vitreous body") by means of the so-called *pre-retinal septum* or *lamella* * discovered by him. Combating Grenacher's conclusions, Graber ('79, p. 66) says: If really the pigment-cells were directly continuous with the retinal cells, as Grenacher's Fig. 31 (Vespa) makes them, then there would be an uninterrupted transition from retina to hypodermis, and consequently the typical two-layer "stemma" could be considered as only a modification of the apparently one-layer eye of the Dytiscus larva. "Eine solche directe Verbindung der Retina," he adds, "mit den das Auge umsäumenden Integumentzellen existirt aber nicht; Hypodermis, Pigment- und Krystallkörperzellen einerseits und Retina anderseits bilden vielmehr je ein geschlossenes Ganzes für sich, indem sich eben zwischen beiden Straten unser präretinales Septum durch und durch zieht, *und so vielleicht auch für die Zulässigkeit der Grenacher'schen Theorie bezüglich des hypodermalen* (wir sagen nicht ectodermatischen) *Ursprungs der Arthropoden-Retina eine schwer zu überwindende Schranke bildet.*" In his *résumé* of the principal results of his paper Graber (p. 88) gives as the second result: "Die Retina des Stemma ist in ihrer ganzen Ausdehnung durch

* I shall in the future refer to this structure as the "pre-retinal *membrane*."

eine besondere cuticulare mit der Sclera zusammenhängende Zwischenlamelle (präretinales Septum) vom integumentalen Epithel (Hypodermis, "Pigment-" und "Glaskörper-" zellen) abgesondert. — Dies spricht (vom rein topographischen Standpunct aus) für die Ausschliessung derselben von der Hypodermis."

Graber's belief in the derivation of the retina from the nervous system rather than from the hypodermis is still more emphatically expressed in his subsequent paper on the eyes of Chætopoda (Graber, 79[b], pp. 280 and 310), where he says of the retina of Alciope: "Dieser [axis] Faden spricht aber auch am meisten dafür, dass die primären Retinazellen, resp. deren mehrkernige Differenzirungsgebilde, oder die secundären Retinapallisaden, nicht *direct* von der äusseren (integumentalen) Zelllage, sondern aus der inneren (secundären) Anlage des Nervensystems sich ausbildet." Concerning the eyes of Chætopods in general, he adds (p. 310): "Der Augapfel als Ganzes besitzt keine eigne Umhüllung (Sclerotica im Sinne der Wirbelthiere und Cephalopoden), wohl aber kommt eine solche dem Retinabecher zu, der als ein selbstständiger Abschnitt vom allgemeinen oder integumentalen Theile abgelöst werden kann. Diese Retina-Hülle ist eine dünne Cuticula und erweist sich topographisch als ein gestielter blasenartiger Anhang der Hirnkapsel." He says further (p. 312): "Die Retina ist in ihrer gesammten Ausdehnung nichts Anderes als die Endausbreitung des Sehnervs," etc.

In the first published abstract of his paper on the structure and functions of the eyes of Arthropoda, Lowne ('83, p. 142) claims that his "Dioptron" of the compound eye apparently corresponds to the cornea, the vitreous, and the fibrous membrane (Graber's pre-retinal lamella) of the simple ocellus. By implication the "Neuron" in the compound eye and that in the simple eye are therefore also homologous. Concerning the origin of these two parts he says (p. 142): "All the structures of the Dioptron are developed from the cellular Hypoderm, whilst all the structures of the Neuron are formed from a solid papilla, or from a number of papillæ which are outgrowths from the Cephalic Ganglia, so that in this respect there is ground for a morphological comparison of the Dioptron with the dioptric structures, and of the Neuron with the nervous structures of the eye of a Vertebrate."

In the paper as ultimately published by Lowne ('84), it is evident that his conclusions relative to the origin of the "Neuron" from the cephalic ganglia are based, so far as his own observations go, upon the development of the *compound* eyes; so that he only leaves it to be *inferred* that, in his opinion, it has in the simple eyes the same origin. It is in that

sense, at least, that I understand the tenor of his criticism (p. 415) of Grenacher's belief: "At present the origin of the retina of the simple eye cannot be said to have been determined; I have sought in vain for any reliable indications as to its origin. Dr. Grenacher believes it to arise by a modification of the cells of the hypoderm. His arguments in favor of this origin are very unsatisfactory, and apparently indicate that the vitreous, and *not the retinal elements*, arise from this layer."

The conclusions reached by Schimkewitsch ('84) place him also with those who regard the retina as an outgrowth of the cephalic ganglia. He says (p. 10): "According to my observations, the eye of Epeira and of other spiders may be divided into two quite distinct parts: one part we call epithelial, the other part retinal or neural. The first embraces a lens and a vitreous body, and is separated from the second by a pre-retinal membrane. The retinal part is formed by a collection of terminations of the fibres of the optic nerve; each termination is formed by an enlargement of the fibre, which supports, in the case of Epeira, a double bacillus and nuclei. The two parts [epithelial and retinal] are enveloped by a membrane — a prolongation of the neurilemma of the optic nerve — which merges into (*se confond*) the subcutaneous connective layer and the pre-retinal membrane (*lame*)." At p. 14 of the same paper he adds: "The existence of a pre-retinal membrane is an argument — and such is also the opinion of Graber — in favor of the development of the retina at the expense of a neural rudiment, and not at the expense of an epithelial reduplicature, as Grenacher supposes.* Besides that, we have the very important observations of Bobretzky, who shows that the retina of the compound eyes of the crayfish is certainly developed at the expense of the neural rudiment." His general conclusion on this matter is summarized in the following words: "Les couches épithéliales et mésodermiques prennent aussi part à la formation des yeux, comme cela a lieu chez les Vertébrés."

In his more recent paper on the embryology of spiders, Schimkewitsch ('84[a]) does not deal with the origin of the eyes.

The answers to the questions concerning *the source* of the retina and *the method of its formation*, now furnished by Locy, seem adequate to

* A part of the argument implied in the above quotations from Schimkewitsch does not appear directly from the quotations themselves, but rests upon his interpretation of "the membrane which merges with the pre-retinal membrane and with the so-called subcutaneous layer." These three structures are, in his opinion, *connective tissue*, and therefore of *mesodermic* origin.

Further along in the present paper this view will be discussed, and an explanation will be offered of what seems to be the cause of the author's apparent error.

settle these conflicting views, — so far, at least, as regards the eyes of the spider-like type. While the formation of the retina from the epiblast, independently of the cephalic ganglia, determines the controversy in favor of those who have maintained its hypodermal origin, the *method* by which it is formed shows that none of his predecessors have in the least foreseen the true course of events.

He has discovered that in both types of retina exhibited by spiders the retinal part of the eye is formed by an infolding. In the *anterior median eyes of Agelena* *— and probably the same is true in all spiders' eyes which fall under the class called by Graber *post*-bacillar, — this infolding gives rise to a pocket which is ultimately detached † from the hypodermis. The two walls of the pocket soon come into contact, so that this infolded, detached portion of the eye is composed of two layers. The layers are of unequal thickness; and while one of them — the thinner and deeper — remains normal, the other, by the process of infolding, becomes *inverted*. The cells of the thick, inverted layer are developed into retinal cells. The bacilli are formed at what were originally the deep ends of the ectoderm cells (Figs. 1, 8, 10, 20–22. Compare Locy, *l. c.* Pl. x.), and therefore in the inverted condition of the layer are in front of the retinal nuclei.‡ In the course of the involution the outer or thick wall of the pocket becomes applied directly to the deep surface of that portion of the ectoderm which lies immediately behind the infolding. This region of the ectoderm is meantime being converted into a so-called vitreous body.

The inversion of the retina proper is a fact of broader significance than would at first appear, and it affords a satisfactory explanation of some of the points in the anatomy and histology of simple eyes which have been so earnestly discussed during the past few years.

After Grenacher ('79) it is especially Lankester and Bourne ('83) who have emphasized the differences between what the latter authors have named monostichous and diplostichous ommatea; but how far they still were from a full appreciation of the real differences is to be gathered both from the name employed — *diplo*stichous for an ommateum composed of at least *three* originally distinct layers — and from the statement that Grenacher had shown in Myriapoda stages intermediate between monostichous and (their so-called) diplostichous conditions. From the latter

* The conditions in the remaining eyes of Agelena are described and discussed on pp. 75 and 94.

† Compare footnote, p. 66.

‡ It seems to me more appropriate to refer the position of the bacilli to that of the nuclei, rather than *vice versa*; and I shall therefore speak of the two types of eyes as pre- and post-*nuclear*, instead of post- and pre-bacillar as Graber has done.

we must infer, it seems to me, that their explanation is equivalent to saying that the "diplostichous" condition has arisen by a gradual sinking down of the retinal area, and a subsequent closing in of the adjacent epiblast to constitute the outer layer of the ommateum. The fundamental difference between such a method and that shown by Locy to exist in spiders is, that, according to the former assumption, there is *no inversion* of the retinal area, whereas in spiders there is a *complete inversion* of the more superficial of the two infolded layers.

It must be left to future observers to ascertain whether any of the monomeniscous eyes of Arthropods are, as seems possible, actually formed in the manner suggested by the condition in the Myriapods; *i. e.*, without the inversion of the retinal area. Meanwhile one examines with fresh interest the conditions hitherto described in order to ascertain, if may be, the probable outcome of future studies.

Next in importance to the presence of two distinct cell-layers,* the presence or absence of Graber's pre-retinal membrane will be significant. In all cases where there is an obvious pre-retinal membrane, and when the "vitreous" is composed of a layer of cells which abut directly (perpendicularly) upon it, I believe there can be little doubt that the retina has been formed by a process of inversion. Such I think is the case in the eyes of all the *Arachnoids* hitherto carefully studied.

The cases among Arachnoids which will at first sight present the greatest obstacle to the acceptance of this view are those of the scorpions; it is therefore to these that most attention will be given.

Graber has given figures and descriptions of the *median* eyes in scorpions, which have been reviewed both by Grenacher ('80, pp. 421-425) and by Lankester and Bourne ('83, pp. 191-193). Their criticisms deal especially with the nuclear conditions of Graber's "Retinaschläuche." His "parietal pigment- and matrix-zone of the retina" was not reviewed by Grenacher, but is considered at some length by his later critics, under the head of "Intrusive pigmentary connective tissue."

* The presence of the third or posterior layer is unquestionably of the greatest importance as a test of an invagination with inversion; but I believe that it may be so reduced in thickness in the adult that the negative evidence of its not having been hitherto found in any particular case should not weigh too heavily in the interpretation. I find, for example, in the case of some adults (Tegeneria, Theridium, Thomisus) that the posterior layer is indicated only by the presence of very thin, flattened nuclei, sometimes so densely enveloped in pigment-granules as to be almost unrecognizable, but occurring at such regular intervals as to leave little doubt about their real nature.

Graber ('79, pp. 84, 85, Figg. 13, 14) found that in the median eyes of Buthus there was left, after the action of caustic potash had made the central portions of the sections paler, a rose-colored granular rim or marginal zone, and that in this zone were to be seen a few, mostly indistinct, nuclei and markings perpendicular to the sclera, which together might serve at first sight to suggest the presence of a tall cylindrical epithelial sclera-matrix. This view Graber definitely puts aside, however, and concludes that the appearance is due to the oblique direction of the section, the apparent epithelium being only the cut-off (anterior) ends of "Retinaschläuche." But inasmuch as there are no other subcuticular (subscleral) structures, these "retinal sacs" have assumed, in his opinion, notwithstanding their other functions, the *rôle* of matrix-cells.

Even without our present knowledge of the manner in which similar eyes arise, this interpretation would be unsatisfactory, because the marginal zone is most sharply marked off from the retina in the *posterior* half of the ball of the eye, and it would be difficult to imagine the course of retinal cells which in this region could be so cut as to give rise to the appearance figured. But I do not doubt the accuracy of the figure in question (Graber's Fig. 14), and believe that its interpretation becomes easy when considered in connection with the probable origin of the retina. If the median eye in Buthus was formed by an involution with inversion of the retina, Graber's "Matrixzone" would be the posterior layer of that infolding, and its gradually merging into the retinal layer in the anterior half of the ball of the eye would be entirely parallel to what occurs in the formation of the "pre-nuclear" eyes in spiders.

Lankester and Bourne ('83) have also had under consideration this pigment- and matrix-zone of Graber, and have arrived at conclusions which are entirely new. It will be most satisfactory to quote their own words upon what they call "intrusive pigmentary connective tissue:" "The structures which we consider as intrusive connective tissue in the central eyes of the Scorpion may be compared to the interneural cells of the lateral eyes. Like these, they are pigmentiferous, and serve to fill up the spaces between the several nerve-end cells and between these and the ommateal capsule. But whilst we regard the interneural cells as ectodermal in origin, . . . we find reasons for considering the intracapsular pigmentary connective tissue of the central eyes of Scorpions as derived from mesoblast, and of the nature of connective tissue.

"We have not embryological evidence for this conclusion, and depend entirely upon the branching, inosculating character of the pigmentary

cells, and upon the analogy of the pigment-cells surrounding the retinulæ of the polymeniscous eyes of Insects and Crustacea, which are very generally held to be of the nature of connective tissue, as also upon that of the 'packing-tissue' to be described below in the central eye of Limulus.

"We are by no means anxious to maintain that the more epithelium-like cells amongst what we are about to describe as 'intrusive intracapsular connective tissue' may not be of distinct origin from other portions of this pigmentiferous framework, and referable to interneural cells of ectodermal nature; but any such distinctions must be based upon embryological facts which we do not possess. In the present state of knowledge it seems most convenient and justifiable to hold that in the central eyes of the Scorpions there are no interneural cells of ectodermal origin, as there are in the lateral eyes, and that their place is taken by intrusive connective tissue" (pp. 191, 192).

I believe the authors will agree with me that Locy has now furnished the embryological facts which, by a fair use of reasoning from analogy, will allow us to affirm with considerable certainty that at least their "epithelium-like cells" (or, as they have in another place called them, "intracapsular pavement" cells) are *not intrusive*, but are derived from the ectoderm, — not, it is true, in so simple a manner as one might have imagined by merely comparing them with the conditions (interneural cells) which they have found in the lateral eyes. There is this fundamental difference between their conceptions and those which are now presented to us: in their view the "intracapsular pavement" cells, even if shown by embryology to be derived from the ectoderm, would still be essentially interneural cells; *i. e.*, such as were *originally interspersed* among the retinal cells (compare their explanation to Fig. 7). But in the present aspect of the case that is not probable; they are distinctly *not* comparable with the interneural cells of the lateral eyes, — assuming that the latter are "monostichous," * — but belong to an *extra-retinal region* of the ectoderm.

What they are functionally, is to be inferred from their pigmented condition. Their position indicates that they are, in addition, the matrix for that portion of the basement membrane which has received the name "sclera."

Whether the "intracapsular epithelium" represents the *whole* of the posterior layer of the infolding, is a question which is intimately con-

* Whether Lankester and Bourne are right in claiming the lateral eyes of scorpions to be "*monostichous*," is quite another question, which will be discussed presently.

nected with the author's theory of an intrusive (mesoblastic) connective tissue.

At least three possibilities may be suggested to explain the inter-retinular pigment-cells discovered by Lankester and Bourne in the *central* eyes of scorpions: (1) They may be developed from indifferent hypodermal cells practically *in situ;* (2) they may be cells which have been detached from the posterior layer of a retinal involution, and have grown in between the retinulæ from behind; or (3) they may be, as claimed by the authors, intrusive mesodermal cells.

If the lateral eyes are really "monostichous," that would seem to afford an argument in favor of the first possibility, the interneural cells of the lateral eyes being really pigment-cells developed *in situ;* and in that case the "inter-retinular pigment-cells" of the central eyes would correspond to the interneural cells of the lateral eyes.

The above-quoted arguments (pp. 56, 57) in favor of the third possibility do not seem to me to outweigh the fact that it is the hypodermis and its derivatives which have in Arthropods the greatest tendency to the pigmented condition.

Finally, the intimate connection between the other pigmented cells and the "intracapsular epithelium" would be favorable to the second view, — at least I cannot regard the intrusion between the retinal elements of pigment-cells *from this source* (posterior layer of the involution) as any less probable than their migration through the "ommateal capsule" and the intracapsular epithelium.*

No one, however, will think of arriving at a conclusive answer to this question by other means than a careful histogenetic study of the developing eyes of some of the scorpions.

So far, then, as regards the median (central) eyes of scorpions, they do not present conditions sufficiently different from those of spiders to prevent a similar interpretation of their parts. With the *lateral* eyes, however, the case is quite different. If the recent researches of Lankester

* There are other indications, besides that of a triplostichous condition, which point to the probability of an involution of hypodermis as a source for all the post-vitreous portions of the ommateum. In the scorpions, as well as in the spiders, the emergence of the optic-nerve fibres is so eccentric (especially in Androctonus) that one might almost venture to predict even the place and the direction of the invagination. (See theoretical considerations, below, pp. 91, 92.)

Perhaps Metschnikoff ('71, p. 225, Taf. 16, Figg. 10, 11) was very near to discovering the true relation of the eyes to the hypodermis when he explained that they appeared as thickenings of the dermal fold which forms an overgrowth over the cephalic ganglia.

and Bourne are to be accepted, it would appear that the lateral eyes present a much simpler type than the median eyes, — so far, at least, as regards the relation of the retinal layer to the hypodermis, the point upon which the interpretation essentially turns.

It is of importance in the consideration of this question that in neither of their figures (Lankester and Bourne, Figs. 2, 3, 4) are the "interneural" cells represented as reaching to the cuticular lens. They form a layer, — uninterrupted except by the narrow nerve-fibre prolongations of the retinal cells, — the individual elements of which are wedged in between *the posterior ends only* of the cells composing the retina. Nothing in this relation stands in the way of these interneural cells being directly compared with the posterior layer of the retinal infolding in spiders' eyes. The only serious obstacle to a direct comparison with *triplostichous* eyes is the absence of a true "vitreous."

The authors affirm with great positiveness the entire absence of the vitreous layer. There are two considerations which make it appear to me possible that Graber in figuring that layer may not have been so grossly in error as they claim. There are great differences in the *thickness* of the "vitreous" in the adult eyes of different Arthropods. (Compare Grenacher, '79, Figg. 28 and 31.) It is possible either that a very thin layer of cells may have been overlooked by Lankester and Bourne, or that, after secreting the substance of the cuticular lens, the "vitreous" cells are in the adult crowded to the margin or completely obliterated.

If, then, it should happen from any cause whatever (*e. g.* the extreme thinness of the layer, or its prompt degeneration and disappearance after secreting the lens) that the "vitreous body" had escaped the attention of these authors, as suggested by Lowne ('84, p. 416), then one might readily conceive that the lateral eyes of scorpions were formed on practically the same plan as the median eyes of the scorpion and the prenuclear eyes of spiders. In that event the cells called by Lankester and Bourne "interneural" would doubtless represent the posterior of the infolded layers.*

Although Graber ('79, Fig. 4) has given a figure of the lateral eye (Scorpio europæus) which in some respects is much less satisfactory than

* If this were the case (compare Lankester and Bourne, *op. cit.*, "Explanation of the small italics in all figures" and explanations of Figs. 7 and 8), the question raised by the authors — whether the "pigmentiferous cells" (*pp*) within the retinal capsule of the central eye were equivalent to the "interneural epithelial cells" (*gg*) of the lateral eyes, or were "intracapsular (intrusive) connective tissue" — would be answered in favor of the former of the two possibilities.

those of Lankester and Bourne, and although he has given no definite description of a sclera-matrix in these eyes, yet one may fairly infer (cf. *l. c.*, p. 77) his belief in such a matrix, and can find in his figure (left side) indications of nuclear structures which easily admit of such an interpretation. These (sclera-matrix?) cells I consider to be, in any event, the equivalent of what Lankester and Bourne have described as "interneural epithelial cells," the nature of which, it will be observed from their figures (Figs. 2, 3) and descriptions, differs considerably in Euscorpius and Androctonus.

But in addition to the considerations presented by Lankester and Bourne, there is another objection to the interpretation here proposed, which at present I am not able to explain. The direct and apparently primitive manner in which the retinal cells are continued into the nerve fibres seems to point to a normal rather than an inverted condition of the retina.

In either event, the nature of the lateral eyes in scorpions is deserving of further study; and it will not be surprising if it is found that they arise by a process of infolding accompanied by inversion of the retina.

Grenacher ('78) has given a figure of an ocellus in one of the *Phalangidæ* which indicates the presence of a distinct layer of cells ("vitreous") in front of the retina; and although he has not seen anything of a layer behind the retina, these eyes present no more serious obstacle to an origin by involution than do most of the hitherto published figures of the eyes of spiders.

The conditions in the eyes of *Myriapoda* leave more room for doubt. Graber, Grenacher, and Sograff are the only authors who have recently given them any considerable attention.

The eyes in Myriapods — aside from Scutigera, in which they are of a conspicuously different type — are *apparently* either monostichous (Chilognatha) or so-called diplostichous (Chilopoda). The latter evidently approach more nearly the conditions found in Arachnoidea, and will be considered first.

Graber ('79, p. 59) claimed their substantial agreement with the ocelli of the Arachnoids and Hexapods. While Grenacher's subsequent work has made much of Graber's description appear illusory, there are still some points in which it is probable that Graber has given reliable presentations of the histological structure. There is, at least, one thing in which I believe his observations deserving of more attention than they

have hitherto received. He has especially defended the cuticular interpretation of the "sclera," and in connection therewith has urged the existence of a cuticular *matrix*. The nuclei of this matrix he has very distinctly, and I am inclined to think very truthfully, figured (Fig. 18, *k*) and described (pp. 64, 84) for Scolopendra. Even Grenacher ('80, p. 441) has granted a conditional assent to their presence, although maintaining that he did not feel entirely convinced.*

To anticipate a conclusion, the grounds of which will be presented later, — in connection with a discussion of the nature of the pre-retinal membrane, — I may say here that the existence of a distinct cell-layer posterior to the retina, and *inside* the cuticular "sclera," appears to me a strong argument in favor of the view that the retina in the Scolopendridæ has been formed by an involution with inversion. If Graber had realized the probable identity of these posterior cell-layers in Myriapods and scorpions, it is possible he might have been saved the expression of his sixth conclusion : "The ends of the retinal sacs [cells] appear to form, at least in part, the matrix of the sclera."

There is a very palpable difference between the figures of the "vitreous" by Graber, and the figures and descriptions by Grenacher ('80, p. 434); nor is there any room to doubt that Grenacher's work is, in most particulars, incomparably the more satisfactory and reliable. But Grenacher finds, if not a layer of uniformly fashioned cells, at least in some individuals of one species (Branchiostoma) a vitreous composed of an uninterrupted layer of cells, which differ from the vitreous cells of spiders, for example, only in the more central position of their nuclei, and the inclination of their axes towards (deep ends away from) the axis of the eye. This exceptional condition of the vitreous — found only in a few individuals — Grenacher brings into relation with the fact that the lens in these cases was only partially developed, and deduces the conclusion that these animals had recently suffered a moulting, and that the increased thickness of the hypodermis and vitreous is simply evidence of increased functional activity. He recognizes the difficulty in the way of

* According to Grenacher ('80, Fig. 8) the pigment-cells which invest the eye have the character of a continuous epithelium such as the posterior layer of the retinal infolding in spiders does at an early stage; but their relation to the thick stratified cuticula (viz. *outside* the latter) forbids a comparison. If Grenacher's account is correct, the Myriapods stand quite alone in having such a continuous mesodermic investment of the eyes.

Compare also Sograff ('80), Pl. III, fig. 17, where a nearly continuous layer of cells is represented outside the thick cuticula of the eye, but inside only isolated nuclei scattered among the nerve-fibres which occupy the space between the cuticula and the basal ends of the retinal cells.

reconciling this condition of affairs with the typical one-layer condition of the ommateum; he seems to consider it, however, as only a phase in the process of formation, which is insufficient to decide whether the eye is to be regarded as a one-layer or a two-layer structure; for he says: "Which of these two conditions, which are alternately realized in the various phases of the life of the individual, shall we assume as the primary, in order to refer to it the other condition (a thing which presents in itself no difficulty)? Here, I believe, the observation of the first rudiment of the development can alone give a reliable answer; I at least feel incapable of deciding solely upon the hitherto accumulated facts."

It might have been unwise for Grenacher, and it may be even now rash for one to hazard a conjecture as to which was the primary condition; but in view of what is now known about spiders' eyes, I think the evidence favors the conclusion that the exceptional cases present the more primitive condition. One or the other of two things is likely to have taken place, — either the retina was formed by an involution which allowed the "vitreous" to be from the first a *continuous* cell-area, or the retina resulted from a depression of the hypodermis, followed by a ring-like ingrowth of vitreous cells from the margins of the depression. The obliquity of the axes of the vitreous cells, as seen in the *finished* eye, might suggest the probability of simple ingrowth; but in these exceptional *growing* eyes, the continuity of the layer, its nearly uniform thickness, and the very slight oliquity of the central cells, while not absolutely incompatible with such an origin, appear to me more favorable to the supposition of a primitively uninterrupted vitreous layer. There is still a wide difference between the one-layer condition figured by Grenacher for Dytiscus larvæ, and the completed eye of Scolopendra. If, as seems probable, Grenacher is right in supposing the exceptional individuals of Branchiostoma to have been engaged at the time of capture in the construction of lenses, the lateral displacement of the vitreous cells had probably only just begun; but even when completed, the "vitreous" and retina still continue to form two essentially distinct cell-layers.

Graber has claimed the existence of a pre-retinal membrane in Myriapods; but Grenacher asserts that he assigned to it an impossible position. It is true Graber has not carefully described, nor very precisely represented it; but I fail to understand how it was possible for Grenacher to speak of it as located in an impossible place. However inaccurately Graber may have described the cell-layers which constitute "vitreous" and retina, they certainly are in contact, even according to Grenacher's own description; and it is along this region of contact that I understand Graber to have located the pre-retinal membrane. Even Grenacher's

own figures (*l. c.*, Taf. XX, Figg. 2–4) seem to me favorable to the presence of a cuticular partition between the two cell-layers under consideration.

If there are some features of the eye in Chilopoda which seem to favor a method of formation similar to that traced in spiders, there are almost none in the case of the Chilognatha, provided the figures by Graber are to be superseded by the account given by Grenacher. Neither Graber nor Grenacher has figured anything that could be compared to the posterior layer of a retinal involution; and Grenacher denies, in addition, the existence of a "vitreous." In brief, according to the latter author, the whole eye is composed of a single continuous layer of cells formed into a cup-like depression; all, except the cells at the margin of the cup, are bacilli-producing elements. Whether all the cells of the depressed region, or only the marginal ones, are engaged in the production of the lens, the author does not suggest. Apparently, the only chance of there having been a distinct "vitreous" in this case, would rest upon the possibility that these marginal cells at first meet in front of the retina, and afterwards suffer a complete centrifugal displacement; but of this there is as yet no direct evidence.

The apparent improbability of an involution with inversion in the case of the Chilognatha is not without weight in considering the nature of the eyes in Chilopoda, since the arrangement of the retinal cells is so strikingly similar in the two groups as to render a fundamental difference between them highly improbable. Further, the almost strictly symmetrical (radial) arrangement of the parts in all Myriapoda stands in contrast to a very common obliquity in the eyes of spiders. So, notwithstanding the several arguments which I have presented in the case of the Scolopendridæ favorable to an involution with inversion, I am not entirely certain that such has really taken place. While the evidence strongly inclines me to a belief in a process of inversion for Chilopoda, I agree with Grenacher that nothing short of a study of the development of the eyes is likely to afford an absolutely satisfactory answer.

I am not able to read Sograff's paper ('80), published in Russian; but in his preliminary paper ('79) he does not seem to have recognized any difference between the structure of the eyes of coleopterous larvæ and of spiders.*

In the case of *Hexapoda* the simple eyes of the larvæ and the ocelli of the adult are sufficiently different to require separate consider-

* "The eyes of the Lithobidæ and Scolopendridæ are exactly like the eyes of the larvæ of Acilius and other Coleoptera, *as well as* those of the spiders" (Sograff, '79, p. 17).

ation.* There are no satisfactory observations on the course of events during development in either of these cases.

The simple eyes of the *larvæ* of Dytiscus and Acilius have figured as types of the one-layer condition since the time of Grenacher's masterly work; and indeed there seems at first sight little or no opportunity for any other interpretation, even though Graber ('80) at first suggested, and then (in a footnote, *l. c.*, p. 67) definitely claimed the existence of a pre-retinal membrane in the case of Dytiscus. But the direct and evident continuity of the "vitreous" cells with the retinal cells, especially the uniformity in the positions of the *nuclei* in the two regions, makes an inversion of the retinal layer extremely improbable. Even in the larger dorsal eyes of Acilius, where there is a perceptible difference in the size of the nuclei in the "vitreous" and the retina, the continuity appears from Grenacher's figure (*l. c.*, Fig. 4) absolutely uninterrupted. There is a striking similarity between this eye and the anterior median eye of Salticus; but the presence of (even a few) nuclei just in front of the anterior face of the retina in the latter case (compare Grenacher, '79, Fig. 28) is sufficient evidence of an interruption in the continuity between "vitreous" and retina in Salticus, and makes a substantial difference between the two at least possible. However improbable a like interruption in the continuity of these cell-layers may be in Acilius, it is not to be overlooked that a complete separation of retina from "vitreous" even here could easily have been followed by conditions like those figured by Grenacher; for to accomplish this it would only have required a subsequent displacement of the basal ends of the "vitreous" cells containing pre-retinal nuclei to the margin of the pigmented cylinder. That such a displacement — accompanied, perhaps, with partial obliteration — has really taken place in the case of Salticus, seems probable from the paucity of the pre-retinal nuclei figured,† and their entire absence from the funnel-shaped depression in the middle of the retina.

Finally, in the *ventral* eye of Acilius figured by Grenacher ('79, Fig. 10), the appearance of the vitreous is certainly not more favorable to a monostichous than to a so-called diplostichous condition. While in the dorsal eyes the basal (nucleated) ends of the vitreous cells abut upon the periphery of the cylindrical ocular mass, in the ventral eyes they appear to end directly in front of the retina, to the surface of which they are almost perpendicular. They consequently appear in the figure to form

* The "compound ocelli" are not so directly comparable with the types of eyes with which the present paper is concerned.

† I can confirm the fact from my own observations.

a continuous cell-layer in front of and concentric with the retina. The critical region — where the pigmented hypodermis passes into the layers behind the lens — is not satisfactorily portrayed in the figure. On one side (the right) the hypodermis seems to be directly continuous with the *retinal* layer; upon the other side it is continuous with the layer forming the *vitreous body*, the retina being on this side more detached from it. Not finding nuclei in the vitreous layer, Grenacher admits that they may have entirely disappeared; but he is more inclined to the opinion that they are grouped with nuclei of the ring-shaped pigmented zone at the anterior border of the retina, — where the nuclei are too numerous to be supposed to belong exclusively to the pigment zone, — and that the finely attenuated posterior ends of the cells, bent outward towards the nuclei, escaped direct observation.

If the nuclei of the "vitreous" have completely disappeared, it is difficult to see how this could be regarded as a monostichous eye. There is nothing, it is true, in the second assumption which precludes the idea that the ommateum consists of a single layer of cells; but it is equally clear that it does not preclude the possibility that the nuclei of the "vitreous" have been displaced towards the margin of the lens; and this would be compatible with a true involution of the retinal cells. I think that such a displacement of the nuclei from the central portion of the "vitreous" — in a manner analogous to that which Grenacher believes to have taken place with the *retinal* nuclei in the case of Salticus (Grenacher, '79, Fig. 25 K) — is more probable than either their total disappearance or their having primitively held a marginal position.

In all these cases there is the opposing argument that no *third* layer of cells was discovered.

The ocelli of the *imagines* also seem from previous descriptions to be destitute of a third layer, — at least no one, so far as I am aware, has claimed it. From one of Grenacher's figures (that of Crabro, *l. c.*, Fig. 34) I infer that a third layer may nevertheless exist as a thin sheet of cells, forming, as in spiders, the matrix of the so-called sclera.*

The only observations on the development of the simple ocelli of the imago are those of Carrière already alluded to. They are too incomplete to serve as a safe guide. I am, moreover, persuaded, from the examina-

* Grenacher ('79, p. 60) speaks of the nuclei as belonging to this fine cuticula, and in the copy of his paper which I have, the (blue) nuclei lie on the *inner* side of the cuticula. Since the "registering" appears to be very accurate for the "vitreous" cells, I have no doubt that the nuclei of the sclera are printed as Grenacher intended, although no mention of their position in relation to the cuticular membrane ("sclera") occurs in the text.

tion of some of the early stages in the formation of the ocelli of Vespa, which Mr. F. A. Houghton is investigating, that a process of involution takes place ; and I believe that here also it will be shown that there is an inversion of the retinal area.*

If the presence of a distinct and continuous layer of " vitreous " cells in front of the retina possesses any weight in favor of an involution after the type of spiders' eyes, then the simple ocelli of adult Hexapods are likely to have followed the same plan of development as the eyes of Arachnoids. That the cells of the vitreous layer are usually so flat and thin that they have sometimes been overlooked, does not in the least diminish their importance as an index to the manner in which the retina was produced. Indeed Carrière ('85, p. 178) has shown conclusively that the cells composing the thin layer which represents the " vitreous " in the completed eye of Vespa, are much reduced in size as compared with their condition during the formation of the lens. The figure which he has given (Fig. 142) of the eye of the wasp during this stage is very instructive, for it shows that, however obvious the continuity of hypodermis and retina may appear in the finished state of the eye (compare Grenacher, '79, Fig. 31), they are separated during this earlier condition by a wide interval, and that consequently the supposed continuity can have no such importance as might otherwise be attributed to it. Although Grenacher has not figured anything which may be fairly taken to represent Graber's pre-retinal membrane, it is evident from Carrière's figure of the earlier condition that retina and "vitreous" are sharply separated by a line which seems to be a continuation of the inner cuticula of the hypodermis, much as in the eyes of spiders ; and Grenacher himself, criticising Leydig's views, has insisted upon the sharp separation of the two cell-layers.

* Since the above was written, Carrière ('86) has published an article in the Zoolog. Anzeiger (Jahrg. 9, no. 217, pp. 141–147), in which he has reverted to the histological conditions of the ocelli in the Diptera and Orthoptera ; but he has not given any further evidence concerning their development.

Postscript. — Under date of June 1, Prof. Carrière writes me that he has arrived (independently) at the conclusion that the ocelli in Hymenoptera and Diptera are formed by a process of involution, but that the infolded region does not become detached from the hypodermis.

It is possible that this difference of opinion is more formal than real, since there is probably no period in the formation of the ocellus, after the earliest stages of involution, during which the involuted portion is not in *contact* with the hypodermis in the region of the "vitreous ;" but the ultimate intervention of the pre-retinal membrane is to me sufficient evidence of an interruption in the original continuity of the cell-layers. That is all I should wish to claim by saying the infolded portion of the hypodermis became " detached " from the permanent hypodermis.

I have referred especially to the ocelli of Hymenoptera because of the evidence of a third layer, and the certainty of there being a "vitreous" which undergoes a great reduction during the development of the eye. Even if a "vitreous" should in some instances appear to be wanting in the adult, the condition could be fairly explained as a result of ultimate atrophy. The evidence for the existence of a third layer is in most cases still wanting. When Grenacher ('79, p. 57) claimed a substantial agreement in the morphology of the ocelli of insects and the eyes of spiders, he based his conclusion on the presence of two distinct cell-layers, — a vitreous and retina. With the present knowledge of the development in the case of spiders, it again becomes an open question whether the morphological change in insects follows the same fundamental plan. It is not impossible that there are among insects two methods of development for the ocelli, — one with, the other without, retinal inversion. A conspicuously reduced "vitreous," and the probable existence of a distinct post-retinal layer of cells in Hymenoptera, inclines me to the opinion that in some cases, at least, there is an inversion.

One of the questions which is most intimately connected with that of the origin of the retina concerns the nature and significance of the *pre-retinal membrane.* In connection with this I shall consider the *inner cuticula* or *basement-membrane* of the hypodermis and the "*sclera.*"

Graber ('79, pp.64–67) was the first to call attention to the existence of a homogeneous cuticula-like membrane ("præretinale Zwischenlamelle") between the "vitreous body" and the retina, and, as we have seen, to lay stress upon its existence as an argument against Grenacher's supposition that the retina was derived from the hypodermis. The question in his mind turned upon the *direct continuity* of the hypodermis (pigment) cells with the cell-layer forming the retina. Such a continuity being precluded by the presence of his pre-retinal membrane, the inference of a hypodermal origin for the retina became for him untenable.

Grenacher subsequently ('80, pp. 429, 430) conceded the existence of such a structure in the case of scorpions and spiders, but was unwilling to follow Graber in his generalization that all "Stemmata" possess this membrane. Unable to disprove Graber's claims in the case of Dytiscus by a re-examination of the subject, he was still unwilling to give them any weight, because Graber "claimed with equal certainty the existence of such a cuticular membrane for Myriapods, but assigned to it an entirely impossible location." But the problem of *reconciling* a pre-retinal membrane with the supposed hypodermal origin of the retina, was not attempted by Grenacher.

While the existence of a pre-retinal membrane, as claimed by Graber, is corroborated for eyes of the "pre-nuclear" type, and its presence made readily comprehensible by the observations of Locy, the conclusions drawn by Graber from this anatomical fact have received the reverse of confirmation. Whether eyes of the post-nuclear type exhibit this membrane, is not so easily determined; but the question will be considered in a subsequent part of the present paper.

Lankester and Bourne ('83, p. 182) apply the name "ommateal capsule" to that portion of the "basement-membrane" (inner cuticula) which lies in the region of the ommateum * of the lateral eyes of scorpions, and then extend the use of the term † to "diplostichous" eyes, so as to cover what has been called by the earlier writers "sclera." Denying the existence of the separate "vitreous" claimed by Graber for the lateral eyes, they of course find in these eyes nothing equivalent to Graber's pre-retinal membrane. In the central eyes, however, it exists as "a strong laminated membrane," forming a septum which divides the vitreous body from the rest of the ommateum. The ommateal capsule, of which the septum, they say, forms a part, is "finely laminated and devoid of nuclei."

The "ommateal capsule" in the lateral eyes of Limulus (*l. c.*, p. 203), "whilst well marked in every other region, is deficient immediately below the retinula, where the group of optic-nerve filaments passes out of or into the capsule." The authors regard this deficiency of the capsule as related to the intrusion of connective tissue into the eye; for it is around the optic nerve that the intrusion appears to take place.

In the central eyes of Limulus they "could not define an ommateal capsule," the intrusive connective tissue being much more abundant than in the lateral eyes; but a vitreous body composed of short cells is separated from the retinal body behind it by "firm membrane," not very clearly indicated in their figures, but apparently continuous with the basement-membrane of the hypodermis.

It seems to me possible that the great difficulties attending the investigation of these eyes account for the fact that the authors have not discovered a post-retinal capsule.

* Compare the quotation in the footnote, p. 50.

† However appropriate this terminology may be for monostichous eyes, it evidently is not sufficiently distinctive in the case of "diplostichous" eyes. It would doubtless be better to adopt a terminology which should express the topographical relation of the basement-membrane to the *retina*. The *whole* capsule might then be called the "*retinal capsule*." In diplostichous eyes the "sclera" could then be called the *peri-retinal* (or better, perhaps, the *post-retinal*) *membrane*, in contradistinction to the remaining portion, already appropriately named by Graber "pre-retinal membrane."

The views held by Schimkewitsch ('84, pp. 8, 9, 12) are widely at variance with those of all the other writers. He is without doubt right in bringing the "inner cuticula," the so-called "sclera," and the pre-retinal membrane into a single category; but misled, as I think, by appearances of the sclera that can readily be explained in another manner, he has concluded that all these structures are *cellular*.*

Schimkewitsch finds that at the point of insertion of the dorso-ventral muscles of the abdomen this "inner cuticula" is continuous with the sarcolemma of the muscular bundles. Reasoning from Froriep's ('78) conclusion that the sarcolemma of the striate muscles in *vertebrates* is to be regarded as connective tissue, he maintains that this internal cuticula in Arthropods must also be regarded as a connective [-tissue] formation. He reaffirms the fact stated by Graber; viz., that this same cuticula is prolonged in the form of a pre-retinal layer, and that it merges with the envelope of the eye ("sclera"), — "although it tends to prove the chitinous nature of this envelope; *but*," he adds, "*nuclei are readily visible in its thickness.*" † Finally, in Lycosa saccata during development there lies beneath the integument, directly under the chitinogenous layer and outside the future subcutaneous muscular layer, a series of very flat cells; and they represent, so he claims, the future "internal cuticula" of Graber.

Neither the nuclei in the thickness of the internal cuticula, nor the conditions observed in the development of Lycosa, are figured, so that it would be very difficult to judge of the value of Schimkewitsch's conclusions, were it not that he *has* figured the same conditions, which recur in the envelope of the eye (sclera). "I have already shown," he says

* MacLeod ('80, pp. 31–34), it is true, has urged a similar proposition respecting the so-called *membrana externa*, or *m. propria* of the tracheal tubes, as well as the basement-membrane of the integument; but his conclusion is based upon theoretical considerations rather than upon satisfactory direct evidence. Until the demonstration in this membrane of nuclei distinct from those of the epithelial cells (chitinogenous matrix) is possible, the question cannot be considered as settled in favor of the connective-tissue nature of the membrana propria of the integument.

Grenacher ('80, p. 26) has also spoken incidentally of the fact that the thin, inner cuticula of the hypodermal cells in the larvæ of Dytiscus are "stellenweise kerntragende;" but I do not understand that he directly commits himself to the opinion that these nuclei belong to cells which have served as the matrix of what he calls "Cuticula," much less to the opinion that this membrane is a cellular structure.

† "La même cuticule interne se prolonge en forme de lame prérétinenne dans les yeux et se confond avec l'enveloppe de l'œil, comme l'a démontré Graber, et je puis affirmer le fait, bien qu'il tende à prouver la nature chitineuse de cette enveloppe; mais des noyaux dans son épaisseur sont bien visibles" (p. 9).

(p. 12), "that Graber's cuticula ought to be considered as a connective [-tissue] layer, and in the envelope of the eyes I have been able to establish oval nuclei (Pl. II, Fig. 4, *nrk*); and I claim that the pre-retinal layer, which is merged with these membranes, is also of connective nature."

The conditions of the eye-envelope are somewhat differently represented in each of Schimkewitsch's three figures illustrating its cellular composition. In one figure (Fig. 4, Pl. II) the nuclei appear to lie on the *outer* surface of the homogeneous membrane; in another (Pl. III, Fig. 4) they are distinctly on the *inner* surface; while in the third (Pl. III, Fig. 11) they are less definitely related to the membrane, a portion of the nuclei appearing simply as thickenings in it. Figure 4, Pl. III, is evidently drawn to the largest scale, and also, I believe, represents more truthfully than the others the relations of the nuclei to the membrane; they are simply *tangent to the inner surface of the double-contoured membrane. I believe they are without the least doubt the nuclei of the cells which constitute the posterior of the two layers resulting from the involution of the hypodermis to form the retina.*

With this explanation of the nuclei supposed to lie *in* the "sclera," the theory of the connective-tissue nature of the "internal cuticula" is deprived of an apparently valuable support, and now seems to rest on quite as unsatisfactory evidence as ever before.

Lowne ('84, p. 415) believes that "the columnar cells immediately beneath the cornea (Grenacher's vitreous) represent the dioptron." "They are separated from the retina by a fibrous membrane which apparently corresponds to the membrana basilaris of the compound eye." This basilar membrane the author has previously defined as a *cuticular* structure. But it is evident from the context that the author rests his conclusions on the peculiar *fibrous* pre-bacillar layer which is found in Salticus, and which Grenacher ('78, p. 51) considered to be composed of fibres from the anterior ends of the *retinal cells.* Lowne, it is true, denies the direct connection (claimed by Grenacher) of these fibres with the marginal ring of nuclei; and adds: "In some of these sections the fibrous membrane has completely separated from the bacilla, just as the membrana basilaris separates from the retina in the compound eye." It should be remembered, however, that Grenacher also found nuclei *in* this fibrous layer, and that Lowne's statement in no way affects the validity of that observation,* nor does he (Lowne) attempt any explanation of the fact.

* From the examination of sections of the eyes of an adult Salticus made by Mr. Locy, and of those of Theridium tepidariorum, C. Koch, by Mr. G. H. Parker, I am able to confirm Grenacher's observation.

I think it is sufficiently evident that this "fibrous membrane" in Salticus cannot be considered the morphological equivalent of the pre-retinal membrane originally described by Graber; for if it were, it would be the only known case in which the pre-retinal membrane was composed of *interlacing fibres* (compare Grenacher, '78, Figs. 25, 27), to say nothing of the occasional presence of nuclei within it. Hence, while I agree with the implied conclusion of Lowne that the vitreous layer and the retina are separated by a *cuticular* structure, I regard his reasons as altogether uncritical, and such as would lead, if logically pursued, to an entirely different conclusion.

Carrière ('85, p. 187), considering it probable that the two layers of the monostichous eyes have originated by a process of *delamination*, as in the compound eyes, finds it in no way remarkable — even though the separation is much more distinct than in the latter case — that the outer layer of the monostichous eye (a genuine epithelium) develops a "Basalmembran" after the manner of the ordinary epithelium of Arthropods. "But this membrane not only *separates*, it also *joins* the upper with the lower layer; at least I have never met a case in which the two layers had become separated from each other." Although not precisely stated, there can be no doubt that Carrière regards his "Basalmembran" as the equivalent of Graber's pre-retinal membrane, and as a cuticular structure.

Locy's observations and the conclusions which directly result from them not only place the retina in a more satisfactory relation to the hypodermis, but also afford at the same time a fair explanation of the condition and mutual relations of sclera, pre-retinal membrane, and the internal cuticula of the hypodermis. It now becomes probable — unless in special cases the reverse is proved by direct observation — in all those instances where a pre-retinal membrane is demonstrable in the adult "stemma," first, that the retina has been produced by an involution of the ectoderm (hypodermis), which has *inverted* the more superficial of the two infolded cell-layers; and consequently, secondly, that the eye is *not simply two-layered*, as supposed by Grenacher as well as all subsequent observers, but is really *three-layered* (*triplostichous*).

In the light of this process of involution the deep cuticular layer ("*Binnen-Cuticula*," Graber) appears in readily appreciable relations. Whether as an "inner cuticula" to the permanent hypodermis and the pigment-cells, as the so-called sclera which invests the retinal bulb, or as a pre-retinal membrane, it is really one and the same thing. These three structures have a like origin, — they are the continuous product of the basal ends of ectoderm cells; and the pre-retinal membrane alone requires

the further modifying statement that it may be double, whereas the others are the result of the activity of only a single layer of cells. Grabers' conception of the "Zwischenlamelle" — as a direct prolongation of the integumental "Binnen-Cuticula," from which the sclera proper branches off on the inner or deep side towards the nervus opticus — is to be so far amended as to make both sclera and cuticula to branch from the "Zwischenlamelle," rather than the sclera and "Zwischenlamelle" to branch from the cuticula. Either conception is to that extent faulty that there is no such thing as a branching off or a splitting, but quite the contrary, — a fusion. It is possible that some of the lines seen by Graber within the "Zwischenlamelle" (and explained by him as the result of the ordinary stratification of cuticular membranes) are indications of the plane along which the fusion between the component layers of this pre-retinal membrane took place.

The brilliancy of the eyes of many spiders, to which Dugès ('36, p. 177) was the first to call attention, was investigated by Leydig, but it has received little or no attention from recent writers.

Leydig ('55, p. 439; '57, p. 254; '64, p. 48) describes the structure which is the cause of this brilliancy as a *tapetum*, which is either continuous, lining completely the fundus of the eye, or, in some species (Clubonia claustraria, Hahn, and Theridium sp. ?), interrupted by a band of black pigment which traverses its middle in wavy lines.*

In Phalangium the tapetum is not continuous, but consists of isolated scales ("Flitterchen"). In still other cases (Lycosa saccata, and several species of Epeira) it forms a narrow band at the anterior rim of the eye-pigment, but becomes visible (as radial streaks lodged in the dark pigment) only after the eyes are dissected out. The tapetum usually consists of scales of the same kind as those which are met with in the tapetum of the fish's eye. They are minute, iridescent plates, which lie close together, and are separable only when subjected to strong pressure. In other cases (Phalangium, Micryphantes) the tapetum is composed of spherules larger than the pigment-granules.

Graber's ('79) account of the tapetum in Tegenaria domestica ("Scheitelauge") is limited to the description of his Figs. 27 and 30. In the former, the "bläulich grün schimmerndes Tapetum" is represented as composed of numerous minute plates, forming a stratum *on both sides of the pre-retinal membrane* (!), the long axes of most of the

* In Clubonia claustraria this black wavy line corresponds, according to Leydig, with the major axis of the oval eye.

plates being *perpendicular* (!) to the membrane. In Fig. 30 the "krystalloide Plättchen" of the tapetum appear as irregular, angular, more or less lozenge-shaped bodies, composed of a granular central mass and a broad rim of uniform thickness, in the substance of which is located the pigment which gives the "Plättchen" their peculiar color.

Graber has apparently fallen into an error both as regards the *location* and the direction of the elements which compose the tapetal layer. It is not likely that the tapetum in Tegenaria differs so fundamentally from that of Agelena. It is probable that Graber has mistaken the posterior ends of the *retinal* cells for the corresponding ends of the so-called vitreous cells.*

Grenacher ('79, p. 55) omitted a consideration of the tapetum for two reasons, — because (1) it presents nothing of importance for the comprehension of the simple eyes and their relation to the compound eyes; and (2) the method of examination would of necessity have been different, since the employment of nitric acid to depigment the eye destroys the tapetum in a very short time, without leaving a trace of it.

Without entering into a discussion of the nature of the tapetum, or its prevalence in the eyes of spiders, I wish to call attention to a few facts which appear to me of deep interest, and possibly of fundamental importance, in any attempt to appreciate the morphological bearings and the functional capabilities of such eyes.

No one, I believe, has hitherto called attention to the distribution of tapeti further than to indicate, as Leydig has done, that certain spiders do, and others do not, possess this structure. My examinations have not been sufficiently numerous to allow a very trustworthy conclusion to be drawn from them; but I have been impressed by the fact that, in the few cases examined, the tapetum, when present, was limited to the lateral anterior and to the posterior eyes; that the anterior median pair does not possess such a layer. When it is remembered that a division of the eyes into two groups is necessitated by the different types of bacillar development,† and that, so far as at present observed, the groups

* *Postscript.* — An examination of sections of the posterior median eyes (Scheitelaugen) of Tegenaria domestica, which Mr. Parker made at my suggestion soon after his return to Cambridge in August, has confirmed my opinion that this species does not differ essentially from Agelena in the position of the tapetum. It is certain that it lies beneath the retinal layer, and is in no sense adjacent to the pre-retinal membrane.

† For convenience of reference I shall call the group embracing only the anterior median pair in Agelena the group with *pre-nuclear bacilli*, or, briefly, *pre-nuclear* group (Graber's post-bacillar); the remaining six eyes in Agelena will then consti-

founded on the position of the bacilli, and those based on the presence or absence of a tapetum, correspond,* one can hardly avoid the conviction that these two features are in some way connected, and that the dimorphism first pointed out by Grenacher is emphasized in other matters than those to which his attention was directed.

The origin of the tapetum and the exact method of its formation are not yet sufficiently clear to me; but I hope to be able before long to acquire more information upon the obscure points. In connection with the development of the eyes of the "post-nuclear" group, Locy ('86, p. 89) has mentioned a structure which separates the two layers of the retinal infolding, and he has described it as a "much-folded chitinous layer, probably homologous with the cuticular covering of the body, with which, in the earlier stages, it appears to be continuous."

After renewed examinations of his preparations, and others of a similar nature from other spiders, I have arrived at the conclusion that this layer is without any doubt the *tapetum*, and that there is no certainty of its having been at first continuous with the external cuticula of the body. As understood by Locy, it was a natural inference, with regard to its formation, that it resulted, like the cuticula, from the secretive activity of the ends of the cells composing one or both the layers of the retinal infolding. This view seems at first to receive confirmation from the early appearance of the tapetum, its apparent continuity (in many cases) with the external cuticula, its greenish-yellow color, and the peculiar shape of the separate elements which ultimately make up this layer. I find also that in Theridium† it is composed of tolerably regular, elongated, hexagonal plates (Pl. III, Fig. 17), neatly fitting edge to edge (as though secreted by a pavement-epithelium); and in one instance I have noticed distinct perpendicular markings in some of the scale-like plates when seen edgewise. If the plates were really comparable with the cuticula, these markings might be the equivalents of "pore canals." I should add, however, that they were so strong as to suggest rather the composition of the plates out of numerous perpendicular rods of uniform size.

But notwithstanding all this, the tapetum may be the result of a cell-

tute the *post-nuclear* (Graber's pre-bacillar) group. If the relation suggested above should be realized, "pre-nuclear" eyes might with equal propriety be designated as *non-tapetal*, and "post-nuclear" as *tapetal*.

* In Thomisus vulgaris, Hentz, I have not been able to find any evidence of the existence of a tapetum either upon sagittal or transverse sections. However, the only sections at my disposal are such as have not been depigmented.

† Theridium tepidariorum, C. Koch.

metamorphosis rather than a simple secretion. Of one thing, at least, I am convinced, — the tapetum owes its origin to a limited number of cells, the nuclei of which become very much elongated during the process of involution. How this takes place can best be shown in connection with a general account of the changes accompanying the formation of the eyes which possess a tapetum.

The hypodermal infolding in the eyes of the "post-nuclear" group was not studied in detail by Locy; it appears to be considerably more complicated than in the case of the anterior median pair. This I have been able to make out from the specimens which Mr. Locy has kindly placed at my disposal.* Most of the figures on the accompanying plates are intended to illustrate these conditions. The first seven figures (Pl. I) present the median faces of successive sagittal sections from the left half of the head of an individual about four days after hatching. The first section is the one nearest the median plane. The directions of the infoldings are such that sagittal sections are more favorable for the study of the posterior median and anterior lateral eyes than for the posterior lateral. The nature of the infolding-process is most readily understood by the aid of sagittal sections of the posterior median eye; and hence I begin the description with that eye.

Of all the sections studied, those which are represented in Figures 8 and 9 (Pl. I) are in some respects the most satisfactory, but in other respects they are possibly misleading. There is a considerable thickening of the hypodermis in two regions, and these two thickened tracts appear to be connected by a continuous row of nuclei (*tap.*) so arranged as to suggest that an S-shaped folding of the hypodermis has taken place. The principal difference between this condition and that described by Locy appears at first sight to be due to the relative thickness of the three components of the "S." In the anterior median eye the middle part is from the beginning the thickest; in the present case it is the thinnest. In one

* This paper was begun in the belief that there was no important difference in the method by which the pre-bacillar and the post-bacillar types of ocelli are developed. After a large portion of the paper was already written, the author received (March, 1886) from Mr. Locy for re-examination the preparations which had served as the basis of his paper. The results of the re-investigation of his material, although not sufficiently complete to form an entirely satisfactory presentation of the subject, are incorporated here because they are deemed of importance, and because to have waited until the questions to which they give rise could have been more exhaustively studied would have necessitated both an extension of the paper beyond the original plan and an undesirable delay in its publication.

of these figures, however (Fig. 9), there is some evidence that the row of nuclei (*tap.*) is not single, but double, and that it is the result of an outfolding of cells (*tap.*) lying between the regions *pr.* and *r.* This conclusion is strengthened by the condition of the *anterior lateral* eye as shown in Fig. 4, *tap.* It is almost certain, from the shape and direction of the nuclei, that the equivalent region in this case is a *fold, open below.* If this middle region really represents a double rather than a single layer of hypodermal cells, then the S-shaped appearance is deceptive; and one must suppose that half of the fold has become merged in one of the thickenings (or otherwise obscured), while the other half remains as the only apparent means of connection between the two thickenings. It is further evident that this *out*folded middle region must be in the nature of a re-entrant fold from the apex * of an original *in*volution, of which the two thickenings constitute the walls.

The condition and connections of this middle region are of great importance in deciding upon the morphological relations of the retina, and it is therefore to be regretted that the evidence as to its real nature is not more conclusive.

In the tract nearest the anterior median eye (Fig. 8, *p r.*) the thickening results simply from a displacement and a slight elongation of the cells and their nuclei, the latter overlapping each other like so many tiles. But the posterior thickening is more complicated; it consists of two parts. The anterior part is composed of cells, the nuclei of which have their long axes nearly parallel with the surface of the head; they collectively form a broad band (*r.*) nearly perpendicular to the surface of the head; the nuclei are wedged between each other so as to form two or three irregular rows. Behind this, and more or less in continuity with it, is a region (*pr r.*) which gradually diminishes from a thickness nearly equalling the length of the "perpendicular band," to the thickness of the ordinary hypodermis. The nuclei in this triangular region are, in the main, perpendicular to the surface of the head, although showing a tendency to radiate from a point near the deep end of the "band." There are, then, four more or less distinct tracts already recognizable. These may be named *from behind forward, pre-retinal* (*pr r.*), *retinal* (*r.*), *tapetal* (*tap.*), and *post-retinal* (*p r.*), respectively. The same regions may also readily

* It is possible that the re-entrant fold was not confined to the bottom (apex) of the eye-pocket, but extended along its *margins*, and that the "fissure" in the tapetum, subsequently referred to, is to be explained as resulting from the failure of these two lateral ingrowths into the pocket to unite along the axis of the latter.

be traced in Fig. 2, although in this section the nuclei of the "band" (*r.*) are more regularly polygonal.

The further changes and the ultimate fate of each of these four tracts seem fairly evident from a simple comparison of this figure (Fig. 2) with Fig. 12, which shows a corresponding view of the same eyes (but from the *right* side of the head) of an individual killed eight days after hatching. (Consult also Figs. 11, 16, 20–24, and the explanations of the figures.) The relative positions of the parts have become slightly changed in the later stage, owing to a continuation of the process of folding and the closer approximation to each other of the three anterior regions.

Numbering from behind forwards, it will be seen that the fourth or last tract (*p r.* Fig. 12) has grown backward until it now lies underneath nearly the whole of the other three regions, and that the first tract (*pr r.*) has grown forward in a corresponding manner, and thus intervenes between the cuticula and the greater portion of the rest of the ocellus. In the place of the third tract (*tap.*) the "tapetum" now appears, with here and there a greatly elongated nucleus, and in the second tract (*r.*) the ends of the cells, which were previously directed forwards, and are now directed downwards, — *i. e.*, toward the tapetum, — have developed the bacilli (*bac.*) characteristic of retinal cells.

From this stage onward, the significance of each of the four layers is evident, and the determination of the homologies with the three layers of the other type is to a certain extent possible.

The *first* or *posterior tract* (*pr r.*) becomes the most superficial layer and secretes the lens (Figs. 12, 22); it is the equivalent of the so-called "vitreous body." * The cell-boundaries in this, as in the other layers, are not made readily distinguishable by the process of preparation employed; but the shape and direction of the well-stained nuclei show that they are quite oblique to the surface of the lens, and that some of them are

* This layer of cells, which I have hitherto called "vitreous body" or "vitreous," in conformity to the prevalent nomenclature, deserves a designation more in keeping with its primitive function, — the secretion of a cuticular lens. Any designation intended to replace so simple a word as "vitreous" must be equally brief in order to be acceptable. I propose the name *lentigen* as a substitute for "vitreous body." I believe this substitution is the more desirable since, according to the best present information, there are probably some cases (*e. g.* Dytiscus) in which "lentigen" and "vitreous body" would not be strictly identical. According to Grenacher's description, certain of the pre-retinal cells in Dytiscus do not abut upon the lens, and their participation in its production may therefore be questioned. They do intervene between the lens and the sensitive surface, however, and may appropriately retain the title "vitreous" cells.

slightly S-shaped. The line of demarcation between this and the second tract, or next deeper layer, is not always sufficiently distinct to allow one to claim with certainty the presence of an internal cuticula (basement-membrane) equivalent to the pre-retinal membrane of Graber. In some cases (Fig. 24) I have seen a sharp limiting membrane between the pre-retinal and retinal layers; but in other cases (Figs. 20–22) it has been impossible to find the least indication of such a membrane. The form and relation of these two tracts indicate a gradual slipping of the first upon the second, rather than a typical folding; but this is probably to be considered as simply a modification of what originally was a true folding at the retino-lentigen margin of the retinal pocket. The *overgrowth* of the lentigenous cells finally results in the same relation between the two tracts as was originally produced by the *ingrowth* (infolding) of the retinal layer. In the original method the retinal layer formed one wall of a *free* pocket (compare Locy, '86, Pl. X, Fig. 64); in the modified process it is from the beginning in contact with the lentigen. The *posterior* region of the latter is finally extended (Figs. 11, 12) so as partially to envelop the posterior margin of the retina.

The relations of the *second tract* (*r.*) are not equally clear upon all the sections. If Figs. 8 and 9 were taken to represent the original unmodified condition of the hypodermal foldings, the conclusion might be that there had been an outfolding having the second tract for its wall on one side, and the third tract on the other. If this were the typical method, there could be no doubt but that that face of the second layer which at this stage is directed forwards, and in which are developed the bacilli, would correspond to the originally *deep* surface of the hypodermis. The bacilli would therefore be developed here, as in the anterior median eyes, at that end of the cells which in the original position of the hypodermis must have been turned *away* from the light. But of the justice of this conclusion I am not convinced; for in other cases (Fig. 4) the *out*-folding, as stated above, appears to involve only the second tract, and in still others there is not sufficient evidence of a true folding of any kind. In Figs. 2 and 16, for example, the conditions are such as might have been produced by a detachment (delamination*) of the cells of the *third* tract (*tap.*) from those of one of the adjacent layers, without the formation of any *out*folding. If either of the latter suppositions represents the true state of the case, then the anterior face of the retinal tract (*r.*)

* The delamination might possibly have resulted from an abbreviation in the process of forming the tapetum, which originally took place exclusively by means of an *outfolding* of the tapetal cells.

corresponds to the *superficial* ends of the component hypodermal cells, and the bacilli accordingly occupy the ends of the cells which were originally directed *towards* the light.

Upon either supposition there is a difficulty in instituting a comparison with the eyes of the "pre-nuclear" group. Upon the first assumption, while the bacilli would occupy the originally deep ends of the cells, as in the other type, the retinal layer as a whole would have been only partially and temporarily inverted, — not permanently, as in that type, — and therefore a strict homology could not be claimed. But upon the second assumption, while the infolding would result in an inversion of the retinal layer, as in the simpler type, the bacilli would occupy the originally *superficial* ends of the cells, and this would also present a serious obstacle to a satisfactory comparison.

I have not, perhaps, a sufficient number of successive stages to place the matter beyond question, but believe that the evidence from the material which I have, and also certain theoretical considerations, point towards the second assumption — *that the retinal layer is inverted* — as the more probable.

In the later stages (Figs. 11, 12, 21–24) it is not always easy to distinguish at once between the nuclei of the first and second layers; but careful attention to the shape and inclination of the nuclei, as well as to the intensity of their staining, allows one to determine fairly well the extent, if not the exact boundaries, of each layer. In Figure 22, for example, the nuclei of the "lentigen" were excessively flattened and apparently degenerating; those of the retinal layer were much paler, less broken, and less granular.

The origin of the *third tract* (*tap.*) is involved in the question just considered; but whatever this origin, — whether it arise by delamination, or by an outfolding which affects only its own cells, or whether it result from an outfolding one wall of which is the retinal layer, — the ultimate condition of this tract can scarcely be called in question; it produces the tapetum. Its nuclei (compare also Figs. 18–22) often undergo a remarkable elongation, and conform in shape to the curved direction of the layer.

In all the eyes of the "post-nuclear" group in Agelena the tapetum has the form of a short canoe, the cavity of which is directed towards the retina. Its greatest length corresponds with the direction of the ectodermic infolding. The end corresponding with the bottom of the pocket of involution is narrower than the opposite end, and does not approach so near to the surface of the head as the latter. The variations in the curvature from end to end are often considerable, amounting in some cases to

a sharp bend in the middle (Fig. 24), and the inclination of the sides to each other may also vary several degrees. The tapetum does not carpet the whole fundus of the eye, being, even in its broadest part, much narrower than the latter (Figs. 13, 14, Pl. III); but it appears to be as extensive as the layer of bacilli developed in front of it. Corresponding in position to the keel of the canoe, is a narrow interruption, or fissure, which extends through the whole length of this layer. It is sometimes slightly curved, S-shaped, and its edges are not always clear cut. It is probable that the appearance which Leydig described as "a band of black pigment traversing the middle of the tapetum" was due to the presence of a similar fissure. In some instances the broad outer end of the tapetum appears to abut directly upon the inner surface of the external cuticula; but even in such cases I have not found in its vicinity any modifications of the cuticula, neither an infolding, nor any marked interference with its regular course. In no case have I been able to trace a direct continuity of cuticular and tapetal substances. Often the tapetum cannot be followed up to the external cuticula; but where the conditions of the sections were favorable for its study, I have never failed to find that the narrow, deep end of the tapetum reaches to, and is apparently continuous with, the internal cuticula, or basement-membrane. This condition seems to afford confirmation of the opinion that the tapetum results from an *out*folding of cells which previously occupied a position at the bottom of an early hypodermal infolding, involving the "retinal" and "post-retinal" tracts. For if the tapetal cells originally grew into the cavity of the hypodermal pocket from its deepest end, they would naturally retain a direct connection with that portion of the basement-membrane where they were at first situated. The region of this ingrowth into the cavity of the original pocket may have extended along the two margins of the pocket for a greater or less distance, and the interruption in the tapetum ("fissure") may possibly have resulted from the failure of these two regions of ingrowth to meet along the axis of the original pocket. The absence of a direct connection with the external cuticula is in itself a strong argument against considering the tapetum homologous with that layer; this is further strengthened by a consideration of the chemical differences between the two, referred to by Grenacher.

The tapetum in Agelena consists of small, thin, slightly curved, scale-like, iridescent structures which are superposed and closely packed. The whole layer has a considerable thickness, and when viewed in longitudinal section, a peculiar wavy, fibrous appearance. If these scales

were the product of a cuticular secretion on the part of the cells of the tapetal layer, one would rightly expect the nuclei of the cells to retain some constant relation to the scales. They should all be located on one or both surfaces of the scale-like layer, or they should all lie in the middle between two sheets of such structures. But I have been unable to find any such constancy of relation, the few nuclei being distributed through the layer apparently without any regard to their distance from either surface of the tapetum (Figs. 15, 18–22, *tap.*). For these reasons I believe it must be admitted that the tapetal scales are formed by a metamorphosis of the cell-substance of the cells forming what I have called the third, or tapetal tract, and not by a process of cuticular secretion. I have not traced the development of the separate scales within the body of a cell, but from the small number of nuclei present it is evident that each cell must give rise to a large number of the scale-like elements.

The *fourth* or *deepest layer* apparently corresponds with the deepest or third layer in the eyes which present the simpler structure, — the pre-nuclear ocelli. There is no doubt that it owes its formation here, as well as there, to a process of hypodermal infolding (Figs. 2, 5–9, 16, 18, 19), and it retains, even after the formation of the tapetum, an evident continuity with the indifferent hypodermis immediately in front of it. Like the deep layer in the eyes of the "pre-nuclear" group, it also becomes the seat of an early and intense pigmentation. That it subserves the ordinary functions of a pigment-layer to the retina can scarcely be doubted; but instead of progressively diminishing in thickness and individuality, as in the pre-nuclear eyes, it here seems to increase in thickness, and may perhaps fulfil important functional relations not shared by the corresponding layer in the simpler ocelli. In the more advanced stages (Figs. 20–24) this layer is considerably augmented in bulk as compared with earlier stages and in comparison with the mass of nuclear material. Its anterior border overlaps the anterior margin of the other layers (Fig. 22), much as the superficial layer (*pr r.*) at an earlier stage (Fig. 12) envelops the posterior margin of the layers underlying it. From its connection with the optic nerve it has acquired a somewhat conical shape (Figs. 23, 24). A portion of the nuclei still forms a more or less continuous layer near the surface (Fig. 20); others (Fig. 22) lie near its axis. Throughout the whole of its substance very fine striations are now distinguishable. The direction of the striations makes it evident that they are due to the radiation of the fibres of the optic nerve, towards which they all tend. But I am not yet entirely certain about

the method of the distribution of the nerve-fibres to the retinal layer. It will require a more careful study of maceration-preparations in connection with sections in different planes to settle this important question. It seems to me improbable that the nerve-fibres pass directly through the tapetum. From what I have seen, I think that most of them pass *around the margins* of that layer to join the anterior ends of the retinal cells, though I have reason to think that some of them reach the retina through the fissure in the tapetum.

The position of the other eyes is not quite so favorable for study by means of sagittal sections; and yet an examination of Figs. 4–6 is sufficient to show that the infolding does not take place in the same direction in both of the lateral eyes. In the anterior laterals the retinal mass lies in *front* of the infolding, whereas in the posterior laterals the retinal mass lies, as in the posterior median eyes, *behind* the infolding.

In the *anterior* lateral eye (Figs. 4, 5) the four tracts are readily distinguishable; and it is necessary only to compare Figs. 4 and 5 with the later stage in Fig. 15, and the still older one of Figs. 18 and 19, in order to learn that the fate of each is the same as in the eye already described; a further description is therefore unnecessary.

That all the layers — especially that producing the tapetum — are not seen with the same distinctness in the *posterior* lateral eye, is, without question, due to the direction of the axis of that eye. The sections are cut in a plane which makes a considerable angle with the main axis of the eye and of the infolding, and the figures therefore give a more oblique view of the cells of the tapetal layer, which consequently are not so readily distinguishable from those of the retina. The earlier sections (Figs. 4, 5) pass through the fundus, — the last (Fig. 7) through the margin of the infolding, where the first and the fourth layers begin to merge into one another. (Compare Explanation of Figures.)

It can be seen from the figures of a later stage (Figs. 13–15) that the axis of this ocellus continues to be nearly perpendicular to the sagittal plane. Of the three sections, that which is nearest the surface of the head (Fig. 13) shows the greater portion of the tapetum,* with its median fissure, nearly *en face;* there are also shown, between the observer and the tapetum, faintly expressed markings nearly perpendicular to the fissure. I could not discover that they were continuous across the region of the fissure. They are undoubtedly due to the differentia-

* A part of the posterior end of this structure was cut away with the preceding section.

tion of bacilli, — the intervals between the markings corresponding very well with the intervals shown when the plane of sectioning is nearly parallel with the direction of the fissure (compare Fig. 19), — but I am uncertain whether it is to be concluded from this that the bacilli have the shape of broad *plates*, or whether these plate-like structures are really composed of *rows of rods*, which the method of preparation and mounting (Canada balsam) has made incapable of optical resolution. There is a suggestive resemblance between these plate-like markings and the sinuous figure formed by the peculiar arrangement of the bacilli in the posterior eye of Lycosa as given by Grenacher ('78, Taf. III, Fig. 24); but I was not able to satisfy myself that these plates presented the folded-back-and-forth arrangement shown in Grenacher's figure. From what is known of the form of the bacilli in other simple eyes, it seems most reasonable to suppose, however, that the plates are composed of rows of bacilli.

The second section (Fig. 14) shows the remaining portion of the tapetum, belonging principally to the anterior end of that structure; if there were portions of the bacilli present upon this section, they were too faint to be discerned.

Finally, the third (deepest) section (Fig. 15) passes entirely below the tapetum, cutting through the post-retinal layer.

The presence or absence of a pre-retinal membrane in the eyes of the present type is of some interest, and yet it may not be of radical importance. Whether the change in the relative positions of the retinal and pre-retinal tracts during development is due to a true folding, or to a slipping of one layer over the other, may depend simply upon how faithfully the original method of transposition (folding) is adhered to. With the gradual substitution of a slipping for a folding, the opportunity for the formation of a pre-retinal membrane may have gradually disappeared; nevertheless, I am of opinion that evidence of such a membrane will usually be found during some stage in the formation of the ocellus.

In some spiders (Tegenaria, Theridium) the development of the retinal infolding and the secretion of the lens are accompanied by a gradual displacement of the deep ends of the "lentigenous" cells towards the margin of the eye, so that in the adult the pre-retinal membrane is almost in contact with the posterior surface of the lens, especially near the margin opposite that towards which the nuclei of the "lentigen" are displaced. This of course increases the difficulty of discerning the membrane.

The method of connection between *retinal cells and optic-nerve fibres* is a fact upon which Grenacher has placed great importance, since upon it depends largely, in his opinion, the interpretation given to the functional value of the individual elements of the retina. According to Grenacher's investigations ('79 and '80) the posterior (deep) end of each cell of the retina (in the "Stemma") is prolonged into a single nerve-fibre, the optic nerve being composed of a bundle of such fibres, presumably as numerous as the retinal elements. This condition — especially well marked in Dytiscus, in the posterior dorsal eyes of Epeira (Grenacher, '79, Figs. 1, 18, 20), in Lithobius, Iulus, and Glomeris (Grenacher, '80, Figs. 9, 11, 13) — has also been confirmed by Lankester and Bourne ('83, Figs. 2, 4, 7, 11) for Scorpionidæ and other Arthropods.

Without being prepared to question the accuracy of the observations of these authors in the cases cited, I am of opinion that there are sufficient reasons for not accepting as universal this mode of union between retinal cells and optic-nerve filaments. I do not wish to be understood as opposing the idea of the independent communication of the elements of the retina with the nerve-centre, but only as claiming that generalizations as to the manner of union between retinal elements and optic-nerve fibres cannot be as quickly and safely drawn as might be inferred from previous writers.

The nature of the optic-nerve connection in the *anterior* eye of Epeira as described and figured by Grenacher ('79, p. 44, Fig. 18, A) is in itself sufficient to raise doubts concerning the universality of the method claimed by him ; viz., a direct prolongation of the (ultimately) posterior ends of the retinal cells. Grenacher says that the peripheral fibres of the optic nerve are continued without sharp limitation directly into the neighboring (" herantretenden ") retina-cells ; but the inner [axial] fibres enter into the interior of the retina, where they divide into two bundles, — a smaller dorsal, and a larger ventral, — which then spread out in single fibres, which in turn join the ends of the corresponding [retinal] cells. That which seems to me unwarranted in his conclusions is, that the axial fibres are joined to the *ends* of the retinal cells. It is not quite clear from the figure cited how this union could be easily effected. The same feature, but in a more marked degree, is also shown in Mr. Locy's sections of the anterior median eyes of Agelena a few days after hatching (Pl. II, Figs. 10, 11, and Pl. V, Figs. 23, 24), and in the adult eyes (anterior median) of Theridium tepidariorum, C.K., which I have examined.

Grenacher himself called attention to a want of symmetry in the eyes

in question (Epeira), the entrance of the optic nerve being slightly dorsal; but the significance of this fact was not perceived by him.

The same peculiarity is also noticeable in the figure of Epeira diadema given by Schimkewitsch ('84, Pl. II, Fig. 4), where, besides, the radiating fibres of the two bundles described by Grenacher are also figured. They are, however, erroneously assumed by the author to be *muscle* fibres.*

In these cases (and doubtless similar conditions prevail in many others) the optic nerve leaves the bulb of the eye not directly opposite the lens, and not always at the point which corresponds to the shortest distance between the eye and the brain. It is noticeable that the place of emergence is in some instances (Figs. 10, 11, 20, 23, 24, *n. opt.*) very near to the superficial border of the retina. If the opinion held by Grenacher were to be substantiated in these cases, we should expect to find the major part of the optic-nerve ramifications bending abruptly backward as soon as they had entered the cuticula of the bulb, and forming behind the bulb a kind of nerve-fibre sheath, which would gradually become thinner

* Schimkewitsch (p. 14) finds in these nerve-fibres the sphincter described by Leydig. "But," he adds, "I have never seen that this sphincter takes its origin from the integument, as claimed by Grenacher. . . . The action of the muscle as a constrictor has been observed by Leydig; but I am not able to understand how the muscle would be able to change the visual axis, [even] if it were attached to the integument, as Grenacher supposes, since the cornea-lens is quite immovable."

Leaving aside the question as to the accuracy of Grenacher's conclusions about a change in the direction of the visual axis, it must be sufficiently evident upon comparing the figures given by the two authors (Grenacher, '79, Fig. 18, M, M′) that the structures in question have nothing in common. Whatever may be the effect of its contraction, the muscle figured by Grenacher encircles the eye, lying, as he expressly states (*l. c.*, p. 46), *outside* the cuticula which invests the eye; whereas that to which Schimkewitsch attributes the function of a sphincter lies wholly *within* the cuticular envelope.

Leydig ('58, p. 441) observed powerful, jerking contractions of the pigmented layer in the eyes of several living spiders. It is a long step that Schimkewitsch has to take when he says Leydig has observed the action of his supposed sphincter muscle. It is the more surprising that he should have adopted such an interpretation of the fibres, when a much more natural one had already been given, as above quoted, by Grenacher. He adduces no argument to prove the contractile nature of the fibres, and, it would seem, must have arrived at his conclusion rather hastily, and without the remembrance of Grenacher's description of the optic nerve.

If it were necessary to strengthen with special arguments the natural interpretation given by Grenacher, one might insist — in addition to the observed direct continuation of the fibres with the optic nerve — upon the absence of transverse striations, and a susceptibility to staining reagents like that of nerve-fibres rather than that of more deeply staining muscle-fibres.

towards the side opposite the place of entrance, as the fibres one after another effected a union with the basal ends of the retinal cells. But nothing of the kind seems to exist in either of the cases cited or in those which have come under my own observation. The fibres, instead of following the surface of the bulb beneath the post-retinal membrane ("sclera"), traverse directly the retinal layer in several groups.* Their connection with the retinal cells, however, is not — as one would fairly infer from Grenacher's account — at the posterior (originally free) ends, but rather with the anterior parts of the cells, † — at least it may be designated as certainly *pre-nuclear*. ‡ The evidence of this rests partly upon the position and general direction of the nerve-strands in a region behind the forming bacilli and in front of the nuclei, and partly on the modification of form which many of the retinal cells and their nuclei exhibit in consequence of this relation. The elongation of the *anterior* ends of the nuclei § is so evidently a result of the peculiar position and connections of the nerve-filaments (Pl. V, Figs. 23, 24) that I cannot for a moment think it attributable to any other cause.

There is also reason to believe that a similar condition exists in the eyes of the "post-nuclear" type, and that the nerve-fibres which *appear* to emerge from the *deep* surface of the retinal layer really pass around the margins of the tapetum (somewhat as in Pecten), to join the now *superficial* ends of the retinal cells This in turn increases the probability of the *inversion* of the retina in "post-nuclear" eyes. (Compare Explanation of Figures.)

I shall return to a consideration of the manner in which this interesting connection is brought about in the pre-nuclear eyes, and of the prob-

* Since the groups do not necessarily lie in the plane of the section, they are not all seen in one section ; but I am satisfied, from the examination of several cases, that such a division of the fibres usually takes place.

† That such a method of nerve-connection with sensory cells is not wholly without parallel, will be evident upon comparing the conditions here described with the account of the termination of the radial nerve of the cochlea in mammals as given by Lavdowsky ('76, pp. 529, 530, Taf. 35, Figg. 10 A, 10 C).

‡ The connection here (after inversion) called "pre-nuclear" is of course equivalent to a post-nuclear connection before inversion. The nerve-fibre, which I believe reaches the nucleus itself, therefore retains as nearly as possible its original method of connection with the retinal cells ; *i. e.*, it approaches the nucleus from what was originally the *deep* end of the hypodermal cell.

§ The nuclei present no such modification of form in the earlier stages of the formation of the eye, before the appearance of the optic nerve, but are similarly rounded at both ends.

able cause of its existence, in the following portion of the paper, devoted to theoretical considerations.

What have been the causes, and what is the real significance, of the hypodermal infolding accompanying the formation of ocelli?

The following speculations are an attempt at the solution of these problems. It is not supposed that they offer a complete explanation of the phenomena, but it is hoped that they may stimulate criticism on the part of future observers, which will ultimately lead to a satisfactory elucidation of the conditions.

The case of *ocelli with pre-nuclear bacilli*, in which there has been an involution with inversion of the retinal layer, will be considered first. One meets here a problem similar to that which is encountered in endeavoring to explain the origin of the retina in vertebrates. If the retina in the ancestors of vertebrates was a patch of ectoderm in its *normal* position, then there are two questions to be settled in explaining the present condition. One is, What could have been the advantage in the assumption of the *inverted* position of the retinal cells in relation to the *direction* of the waves of the light-stimulus? The other, How could the retina have remained functional during the whole of the involution-process which accompanied the formation of the neural tube?

Here, in the "pre-nuclear eyes," the same questions arise: If the retina, which is formed by a process of inversion, was once a normally located portion of the "hypodermis," how could it have remained functional during the process of inversion, and what could have been the motive which led to the inversion?

The question of the immediate cause may perhaps be more readily answered in the case of vertebrates than here; for in vertebrates the ultimate inversion of the retinal cells is only a *necessary consequence* of a much more fundamental change, — the involution of the central nervous system, — which may find its adequate explanation in something (*e. g.* the protection of the nervous system) very remotely, if at all, connected with the functions of the eye. But in the case of spiders' eyes it is different. The retina is formed comparatively late in embryonic life, and, so far as is yet known, independently of any such neural infolding. Unless, then, the retinal inversion can be connected with the formation of the cephalic portion of the central nervous system, the cause of this remarkable complication must be sought in some advantage secured to the eye itself. It is not necessary that the motive be one that is constantly oper-

ating to produce the original result; it is only necessary to show how this influence once operated to bring about the end achieved.

Protection to the retina may have been one of the objects gained; but it is not easy to see how that is better accomplished by an inversion than by a simple depression of the retinal area.

The influence of the light itself, especially the *direction* of the rays which gain access to the retinal cells, may have been more important. Either a gradual shifting in the position of the original lenticular thickening of the cuticula, or the development of a *new* lenticular region, may have been the means by which this new and transforming influence was brought to bear on an already existing retina; for unless the involution can be connected with the formation of the central nervous system, this complicated ocellus must be imagined to have been developed from *a more simple functional eye.*

It is assumable that this primitive eye was composed of a single layer of modified hypodermal cells occupying the normal position (perpendicular) in relation to the surface of the head,* that the proximal (deep) ends of the sensory cells were in connection with the nervous centre by means of nerve-fibres, and that it was in the distal (free) ends of the cells that the bacilli were formed.†

* Either these cells at first all shared in the secretion of the corneal lens, or else this function was confined to a portion of the cells, evenly distributed over the sensitive area, only isolated cells being modified into sensory elements. The latter condition is at present realized in the eyes of many of the invertebrates, and one might at first be inclined to regard it as the result of a differentiation accomplished in the cells of the sensitive area during its development as an organ of special sense. If that were the most reasonable assumption, it would become very doubtful whether the ocelli of Arthropods have ever passed through any such stage of differentiation, unless the lateral eyes of scorpions prove to be truly monostichous, as claimed by Lankester and Bourne. But the results of modern inquiries into the origin of sensory organs have made it more and more probable that this differentiation of epithelium into sensory cells and indifferent cells ("Stutzzellen") is to be carried back to a period which antedates the formation of all special-sense organs. In the light of this important generalization a sensitive area, composed *exclusively* of sensory cells, must be looked upon as a highly modified condition resulting from the atrophy or displacement of the indifferent cells, or, possibly, their gradual conversion into sensory elements.

† There is nothing to favor the supposition that these ocelli were developed from retinal cells which contained bacilli at their *deep* ends before the process of inversion began, for there is not a single case among the invertebrates in which such a condition exists, where other complications do not make it probable that there has been an inversion. The principal cases of "post-nuclear" bacilli are found in the dorsal eyes of Onchydium, and the eyes at the margin of the mantle in certain Lamellibranchs

I know of no example among Arthropods in which this condition is strictly realized, provided the still problematic development of the lateral eyes of scorpions is not taken into consideration. Even the simplest are considerably modified.

It is not certain along what line of modifications the eye with inverted retina has been developed. Not all triplostichous eyes are necessarily like the pre-nuclear type in spiders. A triplostichous condition might be produced by a simple depression of the retinal area and a subsequent closing together of the surrounding hypodermis, ultimately giving rise to an inner and an outer corneal layer, as in many of the mollusks. The condition of the eye in Peripatus suggests such a method of formation in this primitive Tracheate.

It is not unreasonable to suppose, however, that *all* the triplostichous eyes have passed through a condition of simple sac-like depression, in which originally the retinal cells are not inverted, and that from this simple condition two others have originated, — (1) By a closing together and fusion of the lips of the original depression a more or less voluminous cavity (filled with a so-called lens) is formed in front of the still uninverted retina and behind a double layer of hypodermis, — a triplostichous condition such as is realized in Peripatus (Carrière, '85, p. 124; Kennel, '86, p. 32, Taf. III, Fig. 34). (2) By an approximation of the walls of the depression its cavity is reduced to an axial fissure; the cells corresponding to the "outer cornea" in the first case become the "lentigen;" those corresponding to the "inner cornea" become a "vitreous;" the retina still remains uninverted, — a monostichous (potentially tri-

(Pecten, Spondylus, etc.). It seems to me there is little doubt but that in both these cases there has been at some time an inversion of the retinal area. The peculiar course of the optic-nerve fibres and their method of joining the sensory cells (at their anti-bacillar ends), as well as the position of the bacilli, point to this conclusion. They are not, it will be observed, in any sense monostichous eyes.

The eyes of Planarians, also, may possibly be interpreted as having bacilli of the "post-nuclear" type; but here, too, the course of the nerve-fibres points to an inversion of the retina, and, in addition, it is doubtful if the eye is monostichous.

Postscript. — Although Dr. Patten informs me that there is no inversion of the retina in the case of Pecten, I believe that an inversion at some time during the phylogeny of the eyes of Pecten has been the cause of their present condition. But whether there is an inversion during the ontogeny of Pecten or not, the question immediately before us is little affected by it; for eyes like those of Pecten are already too complicated to have served as the primitive condition of the triplostichous ocelli of Arthropods. It may therefore still be safely assumed that the cells of the primitive ocelli had *pre*-nuclear bacilli.

plostichous) condition such as is realized in Dytiscus *as described by Grenacher.*

The triplostichous eye with *inverted* retina may have begun, like that with the normal retina, in the sac-like depression; but it has probably passed through a stage in which there was an early obliteration of the original cavity, as in the second case above. Perhaps the eye in Dytiscus or in some of the Myriapods is the nearest approach — in the hitherto described ocelli of Arthropods — to this earlier condition. Here, at any rate, none of the cells in the retinal area retain the function of secreting cuticula, and the area is therefore relieved from the necessity of a fixed topographical relation to the lens, — an important consideration in the development of the theoretical views which follow

Of the two possible ways suggested, in which a change due to the action of the light may have been brought about, I will first consider that which assumes, — (1) that light gained access to some portion of the periphery of the eye-bulb through other parts of the cuticula than that which originally served for the transmission of light; and (2) that this light from a new direction operated to develop a practically new eye out of *a portion of the already existing retinal cells.*

To make this hypothesis more intelligible, one may begin with the concrete case of the anterior median eye in spiders. (Compare Figs. 25, 26, 30–32.) It may be assumed that the eye from which this "pre-nuclear" type was produced had the form and position * indicated in Fig. 30; that the light which hitherto affected the retina entered through the cuticular lens (*lns.*), in the direction indicated by the arrow, *A;* but that, after the development of the eye up to a certain stage, light also gained access in the direction of the arrow *P* through another region of the cuticula. The same influences which originally tended to the production of an eye underneath the cuticular region (*lns.*) may now have operated on *that portion of the cells of the already formed retina which were directed towards the new lens;* and in time these retinal cells may have developed the characteristic bacillar structures at the ends of the cells *nearest* to this new lens (*lns'.* Fig. 31).

* This primitive eye has been assumed to have occupied the angle of the forehead, as at present (Fig. 11), and to have had its axis inclined to the horizon at an angle of 45°. It might have been parallel with the horizon, or even more nearly perpendicular to it, without having materially affected the problem. If, however, it had been perpendicular, the newly admitted light would have been in front, and the new lens in front of, instead of behind, the original lens, and as a consequence the involution would have been directed forward instead of backward.

The advantages of vision in the new direction may have been due to the more favorable relation of the cells to the *direction* of the newly admitted light as compared with that which came along the original course, inasmuch as the latter was nearly perpendicular to the axes of the retinal cells (and therefore not favorable, upon Grenacher's theory, to the perception of *distinct images*), whereas the former would be parallel to the axes of some of the retinal cells, and therefore competent to furnish (upon the development of the lens) a more distinct image.

Any advantage of this nature would gradually lead to an extension of the favorably located portion of the retina, and even to any modification of the form of the layer as a whole whereby it should be brought into still more favorable optical relations to the newly admitted light. This might be accompanied by a gradual regressive modification of parts of the retina not so situated as to be capable of profiting by light entering from the new direction. In this way the originally symmetrical condition would be replaced by conditions more and more unsymmetrical.*

Thus in time a new lens might be formed and the old one atrophy; one region of the original retina might become converted into a new retina with *new* bacilli at the deep ends of the cells, and the cells of the remaining regions sink from their function of percipient elements to that of simple pigment-cells. The disappearance of the *original* bacilli in the persistently functional area of the original retina might be complete, or only partial.

A strong indication that the anterior median eye in Agelena previously existed in the condition of a functional monostichous eye, the deep ends of whose retinal cells were directly continuous with the optic-nerve fibres, is found in the relation of the optic nerve to the present eye, and especially in its relation at different stages of its growth. Without some such assumption the peculiar connection of the optic nerve with the retina would remain apparently inexplicable; but upon this assumption the conditions appear as a natural consequence of the changes accompanying involution. In the earliest stage in which the connection of the optic nerve with the retina has been figured, before the appearance of the bacilli (Figs. 1, 2), the nerve-fibres emerge from the outer and posterior

* Grenacher has shown that there is an unsymmetrical condition of the retinal cells and their bacilli in the anterior median eyes of Lycosa. (See Grenacher, '78, Taf. III. Fig. 22 A, and text, p. 48.) This must doubtless be regarded as a *secondary* differentiation, — *i. e.* as evolved after the infolding and from a more symmetrical triplostichous condition; but it is instructive as indicating the possibility of regressive changes due to the altered functional requirements imposed on the retina.

border of the retinal infolding *immediately underneath the "lentigen."* Upon the development of the bacilli the fibres emerge farther and farther back from the surface of the head, until finally a considerable interval separates the nerve from the lentigenous cells (Figs. 10, 23, 24, 20). This is exactly what might have been expected if the eye had been developed phylogenetically by *the inversion of a layer of cells which were already in functional activity before the process of inversion began, and the deep ends of which were connected with the optic nerve.** *It is also consistent with the formation at the deep ends of the retinal cells of* SECONDARY *bacilli, which may be regarded as the physical cause of a recession (ontogenetic) of the place where the optic nerve emerges.*

If the fibres of the optic nerve were originally joined to the proximal ends of the sensory cells, it is natural that they should have retained this connection for a longer or shorter period after the beginning of the involution which finally inverted the retina. The nerve-fibres are ultimately connected to post-bacillar parts of the retinal cells. There can be no doubt that the formation of the bacilli is a progressive process; they are not begun throughout their whole extent at the same time, but, beginning at the originally deep ends of the retinal cells, they increase in length by successive additions to the ends of the rods *which are directed towards the nuclei.* It is equally evident that there is a gradual shifting in the region to which the nerve-fibres are distributed, so that this region is always post-bacillar. Nothing seems more reasonable, in view of these facts, than that the secondary condition of the nerve-fibre distribution results from the gradual development of bacilli in the region of the *original* distribution, whereby the nerve-fibres are excluded from their primitive mode of connection with the sensory cells. If this is the true explanation of the cause of the shifting of the nerve-fibres, it offers a valid argument in favor of the *secondary* (*i. e.* recent) origin of the *pre*-nuclear bacilli.

But if these bacilli are not the original rods, what has become of the latter? Were it not for this marked influence of the developing bacilli on the course of the optic-nerve fibres, one might have assumed that the new bacilli were not absolutely new structures, but only the original bacilli migrated from one end of the retinal cells to the other, *pari passu* with the process of retinal inversion, being therefore new only in the sense that they occupy new positions. Such a view seems, for the rea-

* This explanation of the peculiar position of the optic nerve as it emerges from the eye was first suggested to me by Dr. Whitman.

son assigned, untenable. It is more likely that the primitive bacilli have, with loss of function, atrophied, and that consequently the pre-nuclear bacilli of inverted retinæ are not homologous with the pre-nuclear bacilli of uninverted retinæ.

It is possible that the primitive bacilli do not in all cases completely atrophy. There are at least certain problematic bodies in the retina of scorpions which may find an explanation in connection with this hypothesis. I have in mind the structures which Graber described for Androctonus as "posterior nuclei," — subsequently claimed by Grenacher ('80, pp. 423, 424) to be only peculiar, highly refractive bodies, — and the structures which Lankester and Bourne ('83, pp. 185, 193) have seen in the *central* eyes of Euscorpius Italicus, and have described under the name of "*phaospheres.*"

It may be an obstacle that the "phaospheres" are also sometimes found in front of the nuclei, and further, that the rhabdomeres are not formed within, but at the surface of the retinal cells. The variability in the relation of the phaospheres to the nuclei may be regarded as an aberration rendered possible by the loss of function, rudimentary structures being more liable to vary than such as are at the height of their functional activity. (Compare Darwin, Origin of Species, chap. v.) The second obstacle is probably not of great importance, since it still remains to be shown that intra-cellular and extra-cellular rod-like structures are essentially different. Besides, it is conceivable that the *primary* bacilli may have been intra-cellular, while the *secondary* bacilli are extra-cellular.

A more serious obstacle arises from the fact that similar structures (phaospheres) also exist in the *lateral* eyes of Euscorpius Italicus (Lankester and Bourne, '83, p. 185), in the case of which, evidences of an infolding and inversion are not so satisfactory as with the median eyes. If the lateral eyes do *not* result from an infolding and inversion of the retinal layer, this explanation of the "phaospheres" would go for little or nothing, since their presence in the lateral eyes could not be explained on the same hypothesis. I have endeavored, however, to show (p. 59) the great probability of an inversion of the retina in these lateral eyes, and must await a satisfactory disproval of that opinion before allowing this possibility to outweigh the considerations in favor of the explanation of phaospheres which is here attempted.

In the above hypothesis regarding the origin of "pre-nuclear" ocelli, the two points demanding explanation have been kept in view, — the continuance of functional activity, maintained by means of the simul-

taneous operation of light from two directions, and the advantage to vision secured through the more favorable relation of the retina to the direction of the newly admitted light; and there are, in addition, some hitherto unexplained anatomical features which gain by this hypothesis a reasonable explanation.

Changes similar to those imagined above might possibly have accompanied a gradual *shifting in the position of the original lens* (compare Figs. 25–29), rather than the substitution of a new lens. Such a shifting, from whatever cause, might have concentrated the light upon one portion of the retina at the expense of remaining parts. The less-favored parts might have been degraded in functional importance, and might have atrophied. So far not much difficulty would be encountered in appreciating the assumed conditions; but how the light, acting through the original, though shifted, lens, could have afforded any advantage which would have been competent to initiate an inversion, or to carry forward such a process when once begun, is not so easy to comprehend.

In considering the development of "post-nuclear" eyes, however, it will be possible to show how such a migration on the part of the lens may have been an important factor in the process of inversion.

The structure of *ocelli with "post-nuclear" bacilli*, both in the adult condition and in such stages of development as are at present known, is only conditionally referable to what has been assumed above as the primitive state of the eye, and the development is not so easily explained as that of eyes with pre-nuclear bacilli.

The difficulty depends partly upon the uncertainty as to the exact changes through which the eye passes in its ontogeny. Further study will unquestionably soon determine this in a more satisfactory way. But even when it has been definitely established that the retinal layer either does or does not become *inverted*, it will not even then follow that the relations of the two types to each other, and to a primitive antecedent condition, will at once become evident. One naturally looks for a development of both types from a common origin, and, for a time at least, along a common line.

If the retina is inverted, a general comparison with the retina of "pre-nuclear" eyes becomes possible; but the bacilli cannot be strictly homologous, since they do not occupy equivalent ends of the retinal cells.

If the existence of an inversion were established, a common line of development could be fairly maintained; the "post-nuclear" type must then be considered less modified, as far as regards the retina, than the

"pre-nuclear" type: the "post-nuclear" eye *without tapetum* (if such exist) would, to a certain extent, represent a common antecedent of both types, one of which might have been produced by the substitution of new (pre-nuclear) for old (now become post-nuclear) bacilli, and the other by the addition of a tapetum without change in the bacilli.*

On theoretical grounds this seems to be the more probable phylogenetic course; but upon this assumption — that there is an inversion of the retina — the explanation of the motive to the infolding offered above for "pre-nuclear" eyes could not be simply extended to eyes of the post-nuclear type, since the cause of the development of new bacilli in one case, and their non-development in the other, would then be left unexplained.

There are grounds for supposing that the *retention of the original bacilli in "post-nuclear" eyes is due to the development of a tapetum*, — a subject to which I shall return directly.

If the retina is not inverted, even a general comparison with the retina of "pre-nuclear" eyes becomes difficult; for the involution in that event affects only the tapetal and post-retinal layers, not the retina itself. In that case, too, the primitive condition of the eye must be assumed to have been unlike any primitive conditions at present known; viz., with bacilli at the *deep* ends of the hypodermal (sensory) cells.†

If there has been no inversion of the retina, the obstacles to an explanation of the development are considerable. What can have been the cause of an infolding which involves only the tapetal and post-retinal layers, or of the peculiar outfolding between retinal and tapetal layers? I have been unable to form any idea of how this condition could have been produced from a primitively monostichous retina with *post*-nuclear bacilli, consistently with the retention of the functional activity of the eye during all the changes. Neither has it been possible to comprehend, upon the same assumption, how the optic nerve came to emerge from the post-retinal layer.

* But if the retention of the original bacilli in the *inverted* retina was at first directly dependent on the existence of a tapetum, this "common antecedent" condition (without tapetum) would not have been realized, except as the result of a regressive modification of the "post-nuclear" eyes, involving the disappearance of the tapetum.

† It is not entirely impossible that eyes may have arisen which in the primitive, *uninverted* condition possessed post-nuclear bacilli; but it is very improbable that such was the case, because we have not at present, in any animal, a single instance of *monostichous* eyes in which that condition obtains. (Compare the footnote to pp. 88, 89.)

On the other hand, if it be assumed that there has been an inversion, some of the steps in the process appear more easily explainable. Figures 25–29 have been drawn to indicate a possible line of development by inversion, having two stages (Figs. 25, 26) common to this and the "pre-nuclear" type. The direct cause of the beginning of the inversion has been assumed in this instance to be a gradual shifting in the position of the original lens, rather than the appearance of a second lens bringing light from a different direction. The shifting — so one may reason — is accompanied by a gradual atrophy of one side of the retina, the simultaneous development of a tapetum, and a peculiar modification in the course of the fibres of the optic nerve which arise from the persistent portion of the retina.

A lens changing in its relation to the retina, as indicated in the figures, might easily allow a part of the eye to remain functional during the process of inversion; but alone it would afford no explanation of the cause of the inversion, since it would not begin to have an influence (similar to that ascribed to the new lens in "pre-nuclear" eyes) until the change in the direction of the axis of the retinal depression (the thing to be explained) had become sufficient to make some of the retinal cells parallel to the axis of the lens. It must be admitted, then, that, alone, this shifting of the lens is not an adequate explanation. It may be, however, that the formation of a tapetum is the cause, in connection with the shifting of the lens, both for the atrophy of one side of the retina, and the inversion of the other side.

If the formation of a reflecting structure (tapetum) were accompanied by a slight shifting on the part of the lens, the tapetum would practically cut off the light from one face of the retina and reflect it to the sensitive elements of the opposite face. That would result in an atrophy of the part robbed of light, and an increased development of that on which additional (reflected) light fell.

The *direction* of the reflected rays may, in addition, have influenced the *shape* of the retina: if the tapetum were at first a straight band parallel with the original axis of the optic depression (compare Fig. 26), the light falling upon it would be reflected at nearly equal but *very oblique* angles, no matter upon what portion of the band it fell. If, however, the deep portion of the band *became slightly curved* (concave towards the persistent portion of the retina), — as would be altogether natural with an increase in the thickness of the retinal layer on one (functional) side, and a corresponding decrease in thickness on the other (atrophied) side, — the rays reflected from the curved portion of the tapetum would

fall upon the sensitive surface *more nearly perpendicular to it* than they would have done without such a curvature. The advantage of this, even if an increase in the intensity of the light were the only end achieved, is evident; but, in addition to the increased illumination afforded by this part of the tapetum, it is probable that the rays of reflected light would take directions more nearly *parallel with the axes of the corresponding retinal cells* (Fig. 27), and that thus conditions favorable for more distinct vision — perhaps even for the perception of images — would be realized.* Such an advantage once secured at the deep end of the tapetum, it is easy to appreciate how an increase in the extent of the curved portion of the band would enlarge the more successfully reflecting area, thus enhancing the total effect of the light, and possibly affording a more extensive (reflected) image. Once begun, this process would not cease until it had involved the entire eye.

This, it seems to me, would be sufficient to explain the curvature actually found in the adult eyes, where the retinal cells are all perpendicular to the tapetum, and would besides afford *an explanation of the retention of the original bacilli* at the (primitively) free ends of the cells.

It is no longer probable that the iridescent scales of the tapetum are referable to the cuticular secretions of the hypodermis. It is more likely that the tapetum is formed from cells which grow from the apex of the original retinal involution into the cavity formed by that involution, and that they take the form of an outfolding. Whether the tapetal cells, phylogenetically considered, originally constituted a distinct portion of the hypodermis embracing the area corresponding to the apex of the subsequent involution, it is at present impossible to decide; but it seems less probable than that they should have been gradually differentiated from a portion of the retina after the involution (but not the inversion) had begun. It may even be imagined that the tapetal scales in some way represent the metamorphosed bacillar elements of the cells from which they are developed, although I know of no direct evidence of it. Unless they are formed from cells which have previously possessed the function of retinal elements, their source and the cause of their appearance will be still more problematical.

There is reason to suppose that the course of the optic-nerve fibres through the post-tapetal layer is a *secondary* condition. If — as is prob-

* That this curvature finally became so great that the light was reflected outward through the lens, and thus served to help in the illumination of outside objects, does not necessarily interfere with this assumed primitive function of the tapetum.

able from previously presented arguments — these post-nuclear eyes were developed from functional monostichous eyes, the *deep* ends of whose retinal cells were directly connected to the nerve-fibres, the fibres should retain their connection with the deep ends of the cells, and should exhibit, even in advanced stages, a course similar to that pursued by the nerve in "pre-nuclear" eyes at an early stage (Fig. 1). Instead of that they traverse the post-retinal layer, which may have acquired the functions of an optic ganglion in addition to its duties as a pigment-layer. The narrowness of the tapetal band makes it probable that most of the nerve-fibres pass around its margins in making their way from the retina to the post-retinal layer. Although this is a modification of, it is not *fundamentally* different from, the condition in pre-nuclear eyes. In the latter the fibres are collected into a single bundle at the *deep end* of the pocket, and therefore emerge at the *posterior border* of the eye only; in the post-nuclear type the fibres pass over the *lateral margins* of the pocket (and the outer edges of the tapetum) as well as its deep end (compare Figs. 28, 29) before they are joined into a single trunk. The only real difference between the two is in the share which the "post-retinal" layer appears to take in the formation of eyes of the "post-nuclear" type. It is conceivable that this condition may have been brought about gradually during the stages of inversion, — that the nerve-fibres of the aborted half of the eye, instead of undergoing complete atrophy, acquired relations with the persistently functional parts of the retina and their nerve-fibres, and thus influenced the course of the latter.

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EXPLANATION OF FIGURES.

LETTERS.

The following letters are used to designate respectively : —

A.	= Anterior.	*mu.*	= Muscle.
bac.	= Bacillus.	*mu'.*	= Muscle, cut cross-wise.
en e.	= Brain.	*n. op.*	= Optic nerve.
fis. tap.	= Tapetal fissure.	*P.*	= Posterior.
gl.	= Poison gland.	*p r.*	= Post-retinal cell-layer of the eye.
ln g.	= "Lentigen," = "Vitreous" (auct.).	*pr r.*	= Pre-retinal cell-layer.
		r.	= Retina.
lns.	= Cuticular lens.	*tap.*	= Tapetum.

Figures 1–24 were all drawn, with the aid of the Oberhäuser camera, to the same scale (× 515 diam.) from balsam-mounted sections cut from objects stained in alcoholic borax carmine (Grenacher's) and imbedded in paraffine. Figures 1–16 and 18–24 relate to *Agelena nævia;* fig. 17 to *Theridium tepidariorum*, C. K. Figures 1–16, 18, 19, 23, 24 are from preparations by Mr. W. A. Locy; figs. 17, 20–22 from preparations by Mr. G. H. Parker.

PLATE I.

Figs. 1–7. Median faces of successive sagittal sections from the left half of the head of a young *Agelena nævia*, about four days after hatching. The position of the portion of the brain nearest to the eyes is indicated at *en e.*

Fig. 1. The plane of the nearer surface of the section passes through the middle of the anterior median eye, cutting its optic nerve obliquely. The latter emerges from the retina *immediately* beneath the "lentigen." The distal ends of the elongated nuclei in the "lentigen" are scarcely discernible, not being sharply marked off from the surrounding substance, nor so deeply stained as at their proximal ends. Behind the anterior eye, and beyond its optic nerve, are the muscles which separate the posterior median eyes, and then pass obliquely forward and downward, in part beneath the anterior median eye, in part between it and the anterior lateral eye (compare Figs. 2 and 3). Beyond these muscles, and partly obscured by them, is the layer of cells composing the median wall of the posterior median eye. The muscle-cells are traceable through the "hypodermis" to the cuticula at the surface of the head.

Fig. 2. This section embraces a large portion of the lateral wall of the anterior median eye, and the middle region of the posterior median eye. In the latter there are four well-marked regions, — post-retinal, tapetal, retinal, and pre-retinal.

Fig. 3. The lateral wall of the posterior median eye is embraced in this section, so

that the four regions are not as distinctly shown as in Fig. 2. In the post-retinal region (anterior margin of the eye) there is a single cell which differs from the ordinary hypodermal cells and resembles the cells with spherical nuclei found throughout the body-cavity. I am unable to say whether it is a hypodermal cell preparatory to division, or an intrusive element of different origin. The region in front of this eye embraces three successive layers, — nearest the median plane a portion of the lateral wall of the anterior median eye; beyond this, a portion of the muscles above described, distinguishable by the direction of their very large (seen flat-wise?) nuclei; and finally beyond the latter the median wall of the anterior lateral eye. The nuclei of the latter are reproduced in

Fig. 3a, to show more accurately the arrangement of the cells. The four smaller nuclei near the middle of the group correspond in position with the faintly stained nuclei of the tapetum in the following figure, and undoubtedly belong to the tapetal layer.

Fig. 4. This section embraces the middle portion of the anterior lateral eye, the muscular bands which pass between the post. median and post. lateral eyes, and a portion of the median wall of the latter (post-retinal tract). The nuclei of the tapetal region are arranged as though resulting from an outfolding between retinal and post-retinal layers. Most of the nuclei in the anterior layer of this fold are less deeply stained than those of the posterior layer. In this and the three following figures the position of the poison-glands is shown at *gl.*

Fig. 5. The region of tangency between the lateral eyes and their mutual flattening is shown. The post-retinal tracts of both eyes are in contact. The tapetal cells and the post-retinal tract of the anterior eye are separated by the space of the original infolding. The distinction between the different tracts of the posterior eye is not readily to be made out, since the section embraces a part of its median wall; but some of the nuclei near the middle probably are tapetal. In the next section,

Fig. 6, the posterior lateral eye is cut nearly through the middle. The axis of the eye being nearly perpendicular to the plane of the section, the latter embraces in the centre only retinal cells flanked by a few tapetal cells, the latter being separated by a narrow interval from the post-tapetal tract. The lateral region of the anterior eye, which appears in this section, is composed principally of pre-retinal cells.

Fig. 7 shows the extreme lateral margin of the anterior (lateral) eye, and a section of the posterior eye near its lateral margin. In the latter are to be seen in the centre the nuclei of the retinal cells; to the left and beyond them, those of the pre-retinal cells; and to the right the post-retinal cells, separated from the retinal elements by a clear space.

Fig. 8. Lateral face of a sagittal section through the anterior and posterior median eyes of the left side. The tapetal tract appears to be represented by a single row of nuclei. Consult the text, pp. 75–83.

Fig. 9. Median face of a sagittal section through the posterior median eye of the right side. A single faintly-stained nucleus in front of the retinal nuclei apparently belongs to a tapetal cell, and thus suggests the existence of a fold in the tapetal layer. This opinion is strengthened by the prolongation of the other tapetal cells towards the region of the supposed outfolding. The tapering ends of the tapetal nuclei point to the same region, but the lines representing the cell-boundaries have not been printed with sufficient distinctness. Consult the text, pp. 75–83.

PLATE II.

Fig. 10. Median face of a sagittal section through the anterior median eye of the left side, several days after hatching. The bacilli have begun to appear, and the fibres of the optic nerve are seen to be distributed to the retinal cells near their nuclei, — between them and the forming bacilli. The flattened nuclei of the post-retinal tract still indicate the presence of a distinct layer of cells behind the retina. The distance between the place where the optic nerve emerges and the "lentigen" is greater than at first. (Compare Fig. 1.)

Figs. 11, 12. Two successive sagittal sections of the anterior and post. median eyes of the left side (median face) and of the same age as the preceding. The tapetum of the posterior eyes is already formed.

Fig. 11. The optic nerve of the post. eye communicates with the middle of the post-retinal layer. A large portion of the median half of the tapetum removed with this section. The optic-nerve fibres of the anterior eye (not drawn) were distributed, as in Fig. 10.

Fig. 12. The general direction of the original infolding is still evident in the posterior eye. The post-retinal layer is continuous with the hypodermis in front of the eye, and the pre-retinal behind. The bacilli at the anterior edge of the eye are partly obscured by an overlying portion of the tapetum, in which are to be seen the elongated nuclei. Beneath the outline of the anterior eye the optic nerve of the anterior *lateral* eye of the same side is cut obliquely.

PLATE III.

Figs. 13–15. Lateral faces of three successive sagittal sections, through the *lateral* eyes of the *right* side. From the same spider as Figs. 11 and 12.

Fig. 13. Beyond the plate-like bacilli (consult the text, pp. 82, 83) is the tapetum with its longitudinal, uneven fissure, flanked on either side by the nuclei of the retinal cells, which are scanty immediately in front of the tapetum.

Fig. 14. Section through the bottom of the canoe-shaped tapetum of the post. eye, showing the fissure and some of the nuclei of the flanking retinal cells, as well as some of the narrower marginal nuclei of the post-retinal layer. In the anterior eye are to be seen the post-retinal layer and some of the cells of the retina.

Fig. 15. Only the nuclei of the post-retinal layer indicate the posterior eye. The tapetum of the anterior eye is cut lengthwise near its middle. All four layers are distinguishable, the bacilli being already developed.

Fig. 16. Lateral face of a sagittal section through the posterior and anterior median eyes (the latter in outline) from the left side of a specimen one day after hatching, showing the four tracts of the posterior eye before the appearance of tapetum or bacilli.

Fig. 17. *Theridium tepidariorum*, C. K., adult. Portion of a sagittal section — lateral face — passing though the tapetum of the posterior lateral eye of the right side. The outer border of the tapetum is obscured by pigment-granules of the post-tapetal layer, extending outward to the oval outline. The tapetal plates are large and quite regularly arranged; the tapetal fissure is broad and irregular in outline.

Figs. 18, 19. Two successive sagittal sections of the anterior lateral eye of the left side. × *Agelena nævia*, eight days after hatching. The tapetum does not reach the external cuticula.

Fig. 18. The distant surface of the section nearly coincides with the plane of the tapetal fissure, only a small portion of its left half being shown, near the muscle-fibres, *mu'*. The greater portion of the tapetum is seen from behind, and nearly perpendicular to its surface. It obscures the bacilli in front of it. There are five greatly elongated tapetal nuclei still visible.

Fig. 19. The nuclei of the "post-retinal" layer are large and closely packed. Three tapetal nuclei are visible at the edges of the tapetum, which is viewed more nearly edgewise than in Fig. 18. The bacilli are perpendicular to the corresponding parts of the tapetum, and therefore do not all point to a common imaginary centre.

PLATE IV.

Figs. 20–22. Median faces of three successive sagittal sections through the right anterior and posterior median eyes, after the formation of pigment-granules has begun.

Fig. 20. The position of the optic nerve of the anterior eye is sketched in from the two preceding sections. It will be seen that its place of emergence is still farther from the "lentigen" than in Fig. 10. The near edge of the tapetum in the posterior eye shows two elongated tapetal nuclei. The pre-retinal (lentigenous) nuclei are distinguishable from the retinal nuclei by their deeper color, greater flatness, and more granular appearance.

Fig. 21. In the posterior eye five tapetal nuclei are visible, and in the "post-retinal" layer the radiating branches of the optic nerve. The near edge of the bacillar layer is cut; the nuclei of retina and "lentigen" appear as in the previous section.

Fig. 22. In the anterior eye the post-retinal layer has apparently joined the retinal layer. (Compare Fig. 20.) Many of the retinal nuclei present a peculiar vacuolated appearance at their outward ends. The bacilli have attained a greater length than in Fig. 10, their deep ends being covered by pigment-granules. The anterior eye is joined by a muscular (?) band — inserted near the emergence of the optic nerve — to the anterior margin of the posterior eye. In the latter the tapetum reaches the internal cuticula, but not the external cuticula; it contains four tapetal nuclei. Many of the retinal nuclei are elongated, and taper at one end (compare the retinal nuclei of the *anterior* eye in Figs. 23, 24), probably indicating the region of their connection with a fibre of the optic nerve. The bacilli are evidently more numerous than the retinal nuclei.

PLATE V.

Fig. 23. Median face of a sagittal section; anterior and posterior median eyes. The course of the optic nerve to the posterior eye sketched in from the preceding sections. In the anterior eye the fibres of the optic nerve can be traced to the elongated anterior ends of the retinal nuclei, which exhibit shapes dependent on this union.

Fig. 24. Lateral face of a sagittal section through the anterior and posterior median eyes of the right side of the same specimen as the last figure. The distribu-

tion of the fibres of the optic nerve in the anterior eye as in Fig. 23. The post-retinal nuclei still distinguishable, although considerably flattened. In the posterior eye the retinal cells are separated from the "lentigen" by a distinct pre-retinal membrane. Bacilli already well developed in the anterior half of the eye. The tapetum reaches to the external cuticula as well as to the internal cuticula, and contains several tapetal nuclei. The optic nerve and its radiating fibres are shown in the "post-retinal" layer.

Figs. 25-32. Diagrammatic figures to show a possible course of development of the several layers of the simple eyes from the hypodermis. Consult the text, pp. 87–98.

Figs. 25, 26, 30–32. To illustrate the development of eyes of the "pre-nuclear" type. The primary bacilli, at the distal ends of the hypodermal cells, are colored *yellow;* the secondary bacilli, at the (originally) deep ends of the cells, *red.* Optic-nerve fibres are *yellow;* they should have been continued up to the nuclei. Arrows in Figs. 30, 31, indicate the directions of the light from two different sources. (The letters *A.* and *P.* were accidentally omitted.)

Figs. 25–29. To illustrate the development of eyes of the "post-nuclear" type. The primary bacilli (yellow) retained on one side of the eye; replaced on the other side by the tapetum (here assumed to have been developed from the remaining half of the original retina). Optic-nerve fibres, red; they should have been continued up to the nuclei on the side *away* from the bacilli.

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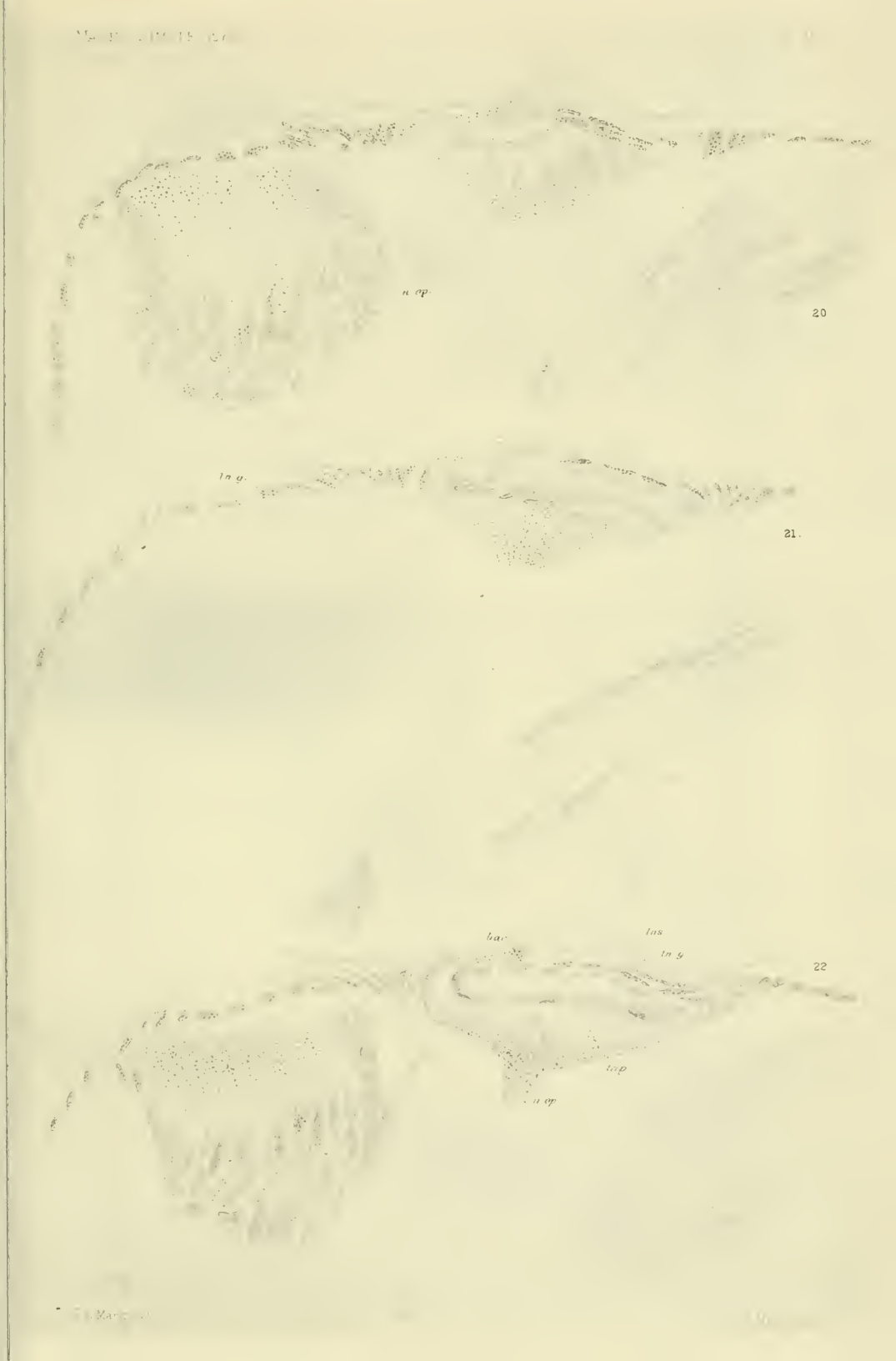
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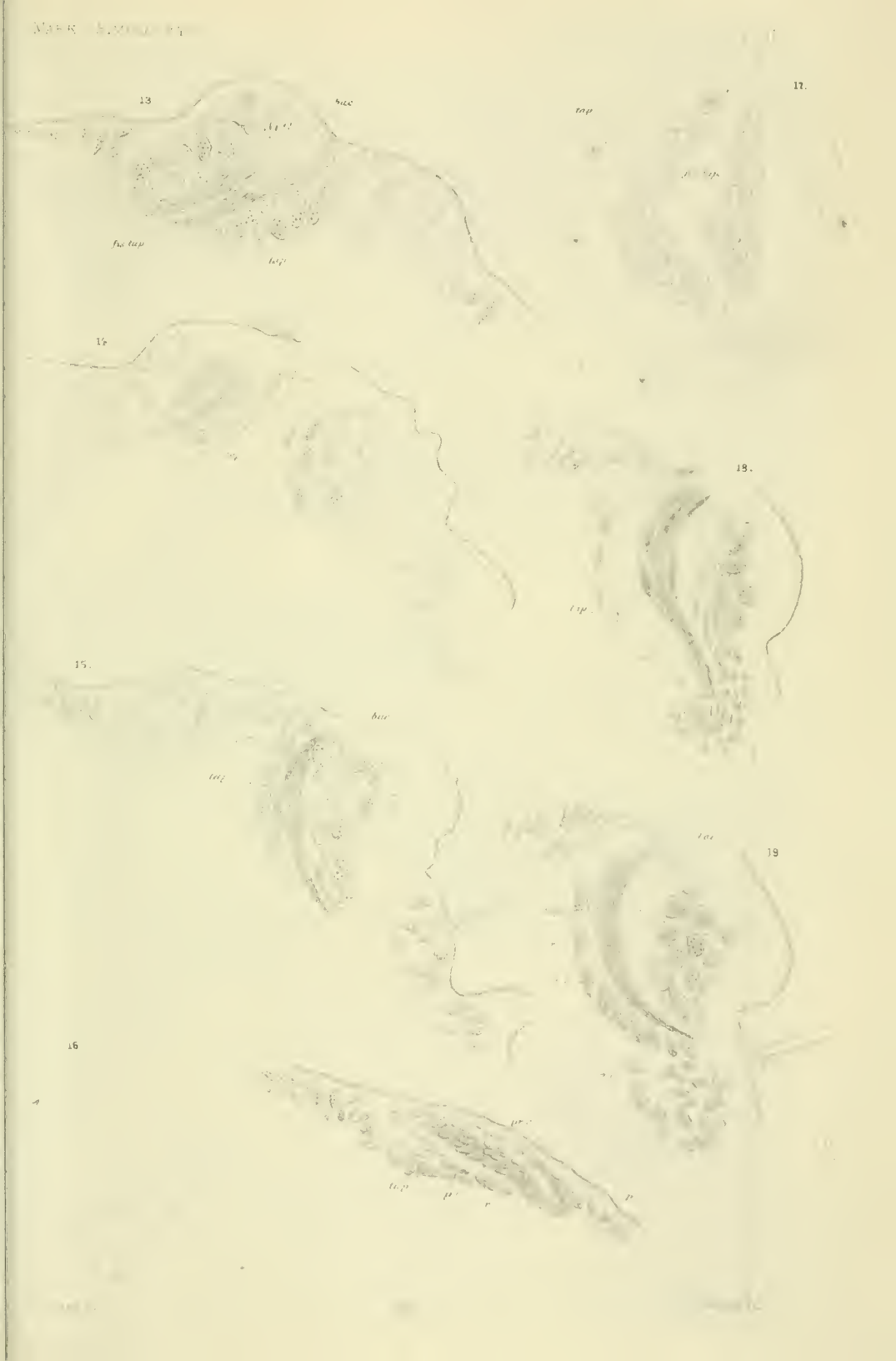
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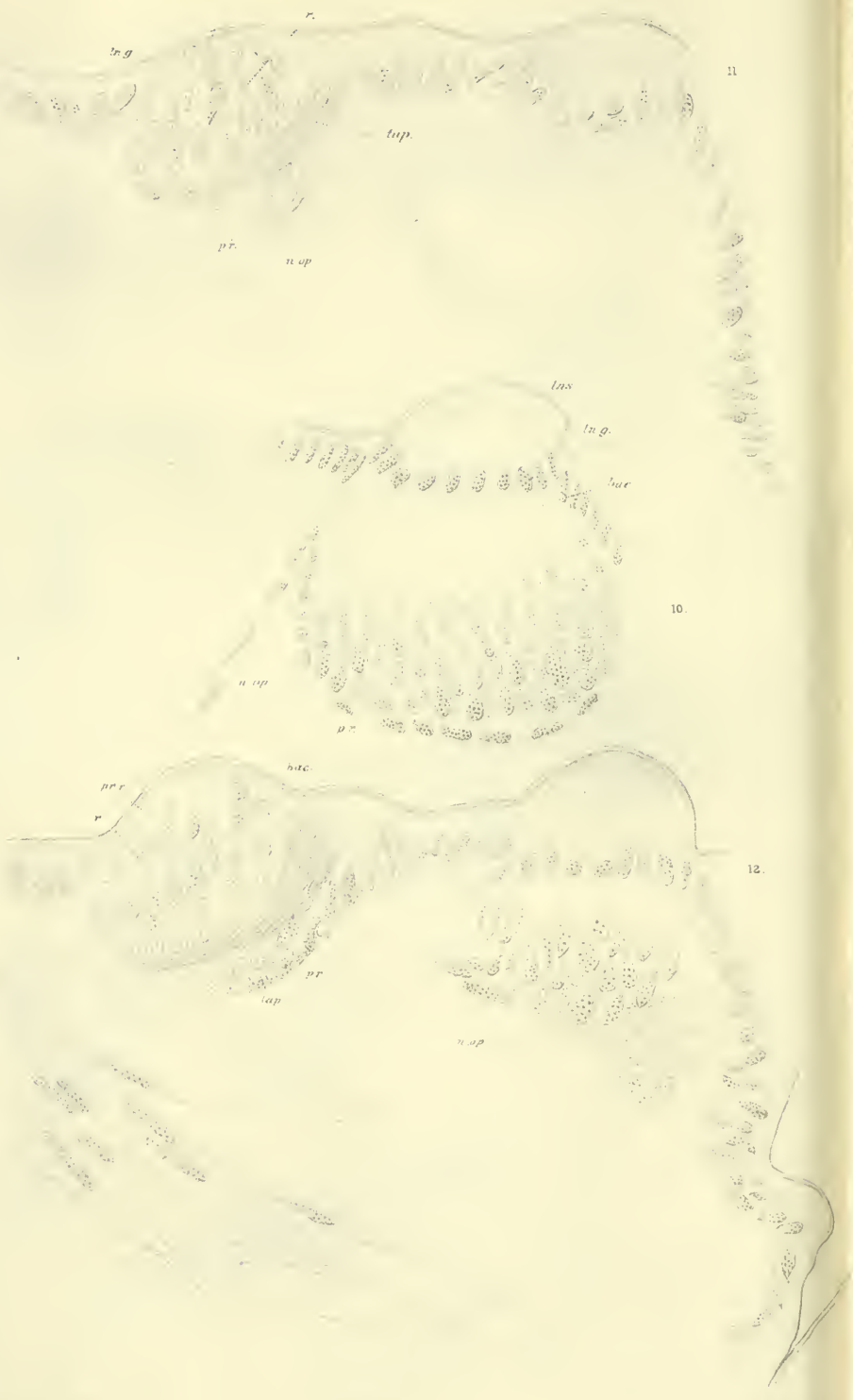
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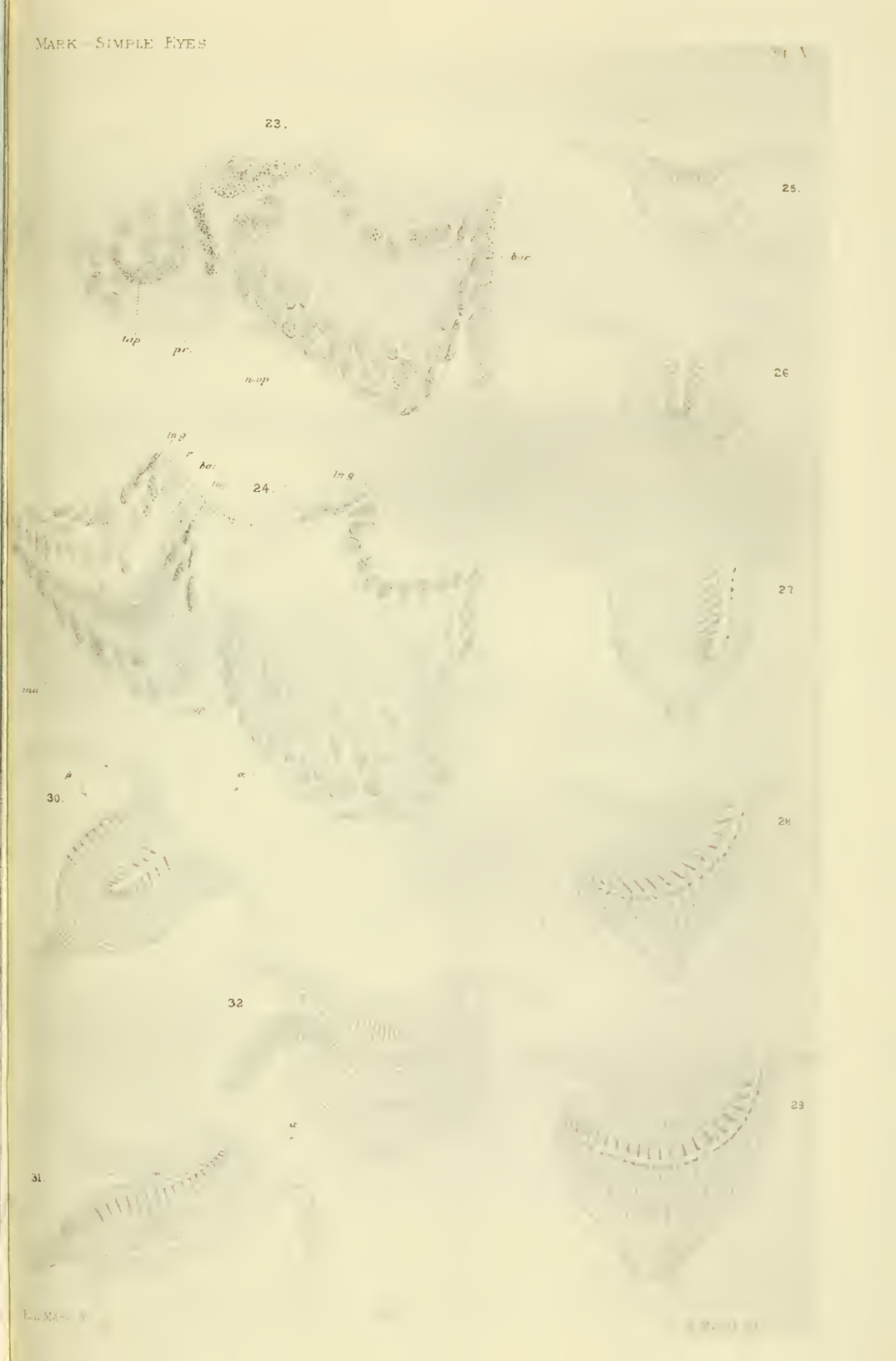
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No. 4. — *Studies from the Newport Marine Zoölogical Laboratory. Communicated by* ALEXANDER AGASSIZ.

XVIII.

On the Development of the Calcareous Plates of Amphiura.

BY J. WALTER FEWKES.

IN a paper published in March, 1886,* it was shown that the egg of Ophiopholis develops into a pluteus-like larva in which the two lateral arms with calcareous rods are well developed. In the month of July of the past summer a similar larva was traced into an adult pluteus. This adult pluteus of Ophiopholis is the same as that doubtfully referred by A. Agassiz to *Amphiura squamata*, thus confirming the statements † made in the paper above quoted. While however it was possible to determine the general anatomy of the adult pluteus of Ophiopholis, circumstances rendered it impossible for me to follow the growth of the calcareous plates and skeleton in the body of the young Ophiopholis forming in this pluteus. It was more convenient to complete my studies of this part of the subject on another genus. For this work the well-known viviparous Ophiuran, *Amphiura squamata*, Sars, was chosen.

This species is well suited for the study. It is common near the Newport Marine Laboratory, and easily collected. It is viviparous, and the young are found in the parents through the months of August and September, when the Laboratory is open for work. Whatever disadvantages come from the possible retardation or acceleration in the sequence of the development of the plates brought about by the abbreviated development, is certainly offset by the ease with which material can be

* Preliminary Observations on the Development of Ophiopholis and Echinarachnius, *Bull. Mus. Comp. Zoöl.*, Vol. XII. No. 4, pp. 105–119. In this paper it was first shown that Ophiopholis has a nomadic pluteus.

† On p. 119 (*op. cit.*) it is said, "*Ophiopholis aculcata* has a development with metamorphosis, passing through a larval stage called the pluteus," and on p. 106, note, "The pluteus referred to *Amphiura squamata* in the 'Embryology of the Echinoderms,' and doubtfully to Amphiura in 'Embryological Monographs,' may be a pluteus of Ophiopholis." The embryology of *A. squamata* is partially traced in the following pages.

procured. My attention in the following observations was chiefly directed to the growth of the hard parts of the body, often called the skeleton, while observations on the bilateral larva are simply introduced as they are thought to throw light on some of the many obscure questions in relation to this part of the subject.

I. GENERAL OBSERVATIONS.

Many observers have called attention to the fact that *A. squamata* is viviparous. No one, so far as the literature has been studied, has seen the young in the American shallow-water Amphiura, although Lyman and others have shown its undoubted identity with the European, *A. squamata.* Of the other species of Amphiura which live in our waters no one has studied the development.

Metschnikoff* has shown that *A. squamata* is hermaphrodite. This observation has been verified by Apostolides,† and I have found the male genital glands in the Newport specimens in the same position as figured by Metschnikoff‡ in the European. Almost every specimen of Amphiura which was collected in August and September was found to contain young, while some had the male glands with lively sperm and young in various stages of growth in the same individual. This fact may look like self-fertilization. It remains to be seen, however, whether the sperm from one individual can impregnate its own ova, or whether this product from another specimen is required for this function. I am not aware that any one has yet succeeded in artificially impregnating an Amphiura with its own sperm. Self-fertilization may take place, but no one has yet recorded it.

My specimens of the adults were found in crevices of the cliffs just below low-water mark. We found good collecting-grounds on the south end of Castle Hill, at Price's Neck, and near Horse's Head, Conanicut Island. The adults prefer a bottom composed of broken Mytilus shells and small stones. Lyman§ has already spoken of their preference for a bottom of broken shells. With a long-handled dip-net a few handfuls of this bottom can be scraped up from the crevices, and the adults can be easily picked out of the fragments of shells with pincers.

* Studien über die Entwickelung der Echinodermen und Nemertinen, *Mém. de l'Acad. Imp. des Sci. de St. Pétersb.*, [7] XIV. 8, pp. 13, 14 (separate copy).

† 1e Thèse. Anatomie et Développement des Ophiures, *Arch. de Zool. Exp. et Gén.*, X. p. 204.

‡ *Op. cit.*, Pl. III. Fig. 1, B. Our *Amphiura squamata* is also hermaphrodite.

§ Ophiuridæ and Astrophytidæ, *Ill. Cat. Mus. Comp. Zoöl.*, No. 1.

The young were taken from the adult by cutting off the disk, leaving the arms intact. By removing the disk in this way it was found that the young remained in it, and when left for a short time in pure water the older specimens crawled into view. Lyman* has recorded that adults found near Bordeaux often in confinement voluntarily cast their disk, from which the orange-colored young emerge. The older forms of the young can voluntarily escape from the disk through the genital slits. Those which have an umbilical attachment, particularly the bilateral larvæ, must be teased from the ovarian attachment by means of needles or small scalpels when required for study. A delicate dissection is necessary to separate the larva from the inner wall of the body without harm to the attached young.

The larvæ were studied alive. Many were killed in weak alcohol, hardened in 93° alcohol, placed in chloroform for three minutes, and then mounted in Canada balsam. The treatment with chloroform brought out the plates with success. Staining in borax carmine showed the water-tubes, but obscured the plates.

Young Amphiuræ were found from the first of August until the end of September, with little reduction in numbers except in the last week. The number of young from different adults varied. Ordinarily a gravid adult would have from ten to fifteen (generally ten) free young, and possibly several bilateral larvæ at the same time. The older young live free in the body cavity, generally with the arms coiled up, but often with an arm extended through the genital slit. Parturition is moderately slow, sometimes rapid. The young when born are orange-colored on the disk, with whitish-colored arms, and with plates less firmly articulated than in the adult. When once born, young were not seen to return to the pouches, nor were they cared for by the adult. They did not cling to the mother after birth. Especial attention was directed to this observation, for I was familiar with the figures given by Thomson† of young Ophiurans of another genus clinging to the disk of the adult.

The young Amphiuræ which voluntarily left the parent were of course

* *Op. cit.*, p. 123.

† Notice of some Peculiarities in the Mode of Propagation of certain Echinoderms of the South Sea, *Journ. Linn. Soc.*, XIII. Dr. W. Stimpson (*Proc. Bost. Soc. Nat. Hist.*, IV. p. 226) found in Charleston, S. C., small Ophiurans clinging to the arms of *Hemipholis cordata*, Lym. (*Ophiolcpis elongata*, Say). He regarded them as the young of the animal to which they were clinging, and thought that they "correspond" to the genus "Ophionyx, M. T."

Lyman (Challenger Ophiuroidea, p. 157) describes and figures two stages of the young Hemipholis which he finds clinging to the arms and disk, and "suspects" that the genus is viviparous.

in confinement in glass aquaria, which condition must be given its proper significance, and may have deterred them from clinging to the parents. In this connection let me mention an observation which has been repeatedly observed in dredging our common "basket-fish." The egg and early development of this animal (*Gorgonocephalus Agassizii*) is unknown, but the young with arms with a single bifurcation have repeatedly been brought up from the bottom clinging to the disk of an old adult. It is very necessary to find out whether or not the basket-fish is viviparous, as this would possibly indicate.

The young Amphiuræ are born at intervals, in a continuous series, not all at the same time. There are well-developed young of different sizes in the same parent. It was not possible to tell from the size, in all cases, whether the mother or adult had young in the body. Swollen specimens were ordinarily gravid, but many large specimens were without young.

When the disk of many swollen specimens was looked at from above (abactinal region), one or more of the interradial regions was observed to have a reddish color and to be more swollen than the remaining. On dissecting these specimens to learn the cause of the color and apparent abnormal condition, they were found to harbor in their bodies bundles of claret-colored ova. The development of these ova in the Amphiura was traced by opening several specimens. Eggs were found in all conditions of cleavage and larval growth, from very young specimens to an adult Crustacean (Copepod?). They are parasitic in nature, and pass their early life in the body of the Ophiuran. In several instances the ova of Amphiura were found with the ova of the parasite, but in most cases an amorphous reddish mass indicated the possible position of the ovarian gland of the host. The ova of the Ophiuran and those of the parasitic Crustacean can be readily distinguished by a difference in color which is well marked. The eggs of the Crustacean are found in bright red or pink clusters. Those of the Amphiura are red and orange, and not in free packets.

The ova of the Crustacean are unattached to the parent. They are often found without parent Crustacean. The development of the parasite will be treated in a special paper. None of the many attempts to produce artificially two Amphiuras by cutting the disk in halves led to positive success, although a six-armed Amphiuran cut in such a way that three arms were left in each half of the body lived as two individuals for a considerable time. They were not observed, however, to bud off new arms, as it was hoped they would do. Embryos with four and six arms were repeatedly found. Adults with six arms were common.

The disk in several instances was removed from its connection with the arms, and the five remaining connected arms lived for three days after the mutilation.

I had some difficulty in identifying the adult Amphiura, from the fact that in some of the best descriptions of *A. squamata* the color of the live animal is not given, while in others it is recorded as white.* None of the adults of *A. squamata* studied were white, but all were brown or chocolate colored when alive. Variation of color is great among specimens of the same genus, and in some localities this species may be white; but the specimens which were studied were not white.

II. THE BILATERALLY SYMMETRICAL LARVA.

August Krohn† and Max Schultze‡ first found out that *Amphiura* (*Ophiolepis*) *squamata*, Sars, is viviparous; and that discovery has been established without possibility of doubt by Sars,§ Lyman,‖ Metschnikoff,¶ Apostolides,** Ludwig,†† and others. Its viviparous life falls into the following divisions: (1) The development of the bilateral larva;

* Packard states (Zoölogy, p. 111): "*A. squamata*, Sars, has long slender arms and is white." In Agassiz's "Sea-Side Studies," p. 115, *A. squamata* is spoken of as the "white Amphiura."

The adults were identified by comparison with specimens in the Museum of Comp. Zoölogy identified by Mr. Lyman, and by reference to published descriptions. Prof. Verrill has also examined my specimens of the adults, and verifies my identification.

† Ueber die Entwickelung einer lebendig gebärenden Ophiure, *Arch. f. Anat. Physiol. u. Wiss. Med.*, 1851. Krohn first showed that *Amphiura* (*Ophiolepis*) *squamata* is viviparous.

The first naturalist to describe the young of *Amphiura* (*Ophiolepis*) *squamata* was Joh. Müller (*Arch. f. Anat. Physiol. u. Wiss. Med.*, 1851, p. 1 *et seq.*). He erroneously ascribed to Ophiolepis in this place a pluteus form. Following Krohn's paper (*op. cit.*, p. 353), where *Ophiolepis* (*Amphiura*) *squamata* is shown to be viviparous, it is acknowledged that the young described by Müller is of some other Ophiuran, and not *Ophiolepis squamata*.

‡ Ueber die Entwickelung von *Ophiolepis squamata*, einer lebendig gebärenden Ophiure, *Arch. f. Anat. Physiol. u. Wiss. Med.*, 1852.

§ Jahresbericht of Leuckart, 1865, p. 86.

‖ Ophiuridæ and Astrophytidæ, *Ill. Cat. Mus. Comp. Zoöl.*, No. 1.

¶ *Op. cit.*, p. 13.

** *Op. cit.*

†† Zur Entwickelungsgeschichte des Ophiurenskelettes, *Zeit. f. Wiss. Zoöl.*, XXXVI.

and (2) The development of the pentagonal or stellate young, free in the body of the parent.

The youngest embryo of Amphiura which was observed by me is a blastosphere.

Blastosphere. — The blastosphere (Pl. II. Fig. 1) was found free in the body of a dissected adult, and had probably ruptured its connection with the parent. It closely resembles the blastosphere of some other Echinoderms, and is of about the same age as that of Amphiura figured by Metschnikoff* and by Apostolides.†

The few blastospheres of Amphiura which were found were unattached to the body walls or to each other. In later stages, as in the bisymmetrical larvæ, the young Amphiuræ are attached by a structure called the umbilicus. Sir W. Thompson has spoken of the free young of certain viviparous Echinoderms in the body cavity of adults, in his "Notice of Peculiarities in the Mode of Propagation of certain Echinoderms of the Southern Sea." ‡ as not appearing to have in any case an organic connection with the parent. It seems natural to suppose, if the bisymmetrical larva is attached, that the younger stages are not free; but I have no proof of this. It is supposed, not proven by observation, that the blastosphere is broken from its attachment.

The cells of the blastosphere are surrounded by two envelopes (m^1, m^2). I am unable to prove that either of these envelopes is "chitinartig," as Metschnikoff describes the apparently homologous outer envelope. The inner envelope resembles somewhat the cortical layer which I have described in the ovum of Ophiopholis where it is believed to be homologous to the *zona radiata* of other Echinoderms. Both envelopes are transparent. Diameter, .13 mm. The blastodermic cells are spherical, red in color. There is no ciliation on the outer surface of the blastodermic cells. Nucleus of each cell well seen. There is a segmentation cavity (*cav*) as in other Echinoderms.

Gastrula. — There is no free nomadic gastrula in Amphiura, but the blastosphere is followed by a larval condition (Pl. II. Fig. 3), in which we recognize certain characters of a gastrula. According to Metschnikoff,§ directly after the blastosphere stage there appears in the protoplasm of the blastodermic cells two layers of cells, "von denen die

* *Op. cit.*, Pl. III. Fig. 3. The "cavity" is lettered *v* (no explanation) in Pl. III. Fig. 5; *cs* in Fig. 4 (*cs*, Fig. 4, is the segmentation cavity).

† *Op. cit.*, Pl. XII. Fig. 9.

‡ *Journ. Linn. Soc.*, XII.

§ *Op. cit.*, p. 14.

untere körnig und roth die obere dagegen glassartig und homogen erscheint." A stage similar to his is figured in Pl. II. Fig. 3. The mode of formation of the cavity is not made evident in either Apostolides' or Metschnikoff's account. The inner layer of cells, or the red cells, is supposed to be the mesoblast; the outer, the epiblast; and the walls of the cavity, or hypoblast, are concealed by the mesoblast. It is possible that hypoblast and mesoblast have as yet not differentiated themselves in the red cells. The blastosphere unquestionably has a true segmentation cavity, but by the concentration of the pigmented cells near its interior, by which concentration the superficial layer (epiblast) of transparent cells appears to be separated, renders the interior of the egg so opaque that observation of the contents is almost impossible without cutting sections. As only one blastosphere and not more than four gastrulæ were found, my material was limited. The transparent outer layer (*ep*) is probably the epiblast, and the masses of reddish cells in the interior of the body of the embryo may be the same as the so-called amœboid or mesoblastic cells in other Echinoderm embryos. The true hypoblast either is not separated from the red cells or is differentiated from them and hidden by these opaque cells. There is what appears to be an external opening (*a*) passing into the opaque region of the ovum, which fact would seem to indicate the existence of a cavity. Unfortunately, however, I am not sure that such an opening exists. Apostolides, however, has described and figured this opening, and there is no reason to doubt its presence. It is necessary to have new observations on the existence of this primitive opening and the way it is formed. It disappears early in larval life. The mode of formation of the hypoblastic wall of the cavity of the gastrula of Amphiura has been interpreted in two ways. The first, and that which would seem the true one from what we know of other Echinoderms, is the embolic method; the second by delamination, unknown elsewhere in the group, is very exceptional and peculiar. Apostolides* supposes that in Amphiura the hypoblast is formed by a delamination of the blastodermic cells and not by invagination. Metschnikoff† says that it is formed by invagination. It is probable that the true blastopore was not observed by this naturalist, and the invagination which he observed was that of the mouth and possibly the œsophagus. This, however, does

* *Op. cit.*, pp. 25, 192.

† *Op. cit.*, p. 14, Pl. III. Fig. 6. A cavity with hypoblastic walls between it and the cutis (*c*) must have existed, as he speaks in the text of such a cavity ("Darmanlage"). His figures do not well represent the hypoblast.

not prevent our accepting the theory that the cavity of the gastrula is formed as Metschnikoff supposes.

In Ophiopholis it has already elsewhere been shown that the archenteron is formed by embole, and the known law of development in other Echinoderms would point to the same method in Amphiura. If there is an invagination of the blastoderm to form an archenteron in Amphiura, it is more masked than in Ophiopholis, and at present it is not possible for me to say whether Apostolides' or Metschnikoff's view of the mode of formation of the archenteron is the correct one. It looks very much as if the epiblast is separated from the reddish layer by a delamination, but it must be remembered that Amphiura is a viviparous genus, and possibly has a highly abbreviated * development in its early history. We may consequently suppose that more or less modification or concealment in the embolic mode in which the archenteron is generally formed in Echinoderms has resulted. It must also be remembered that the majority of gastrulæ of Echinoderms are embolic. My observations support in part Apostolides' statement that the primitive cavity, not however the segmentation cavity, of the gastrula is the intestine ("anus embryonnaire") of the future pluteus. Probably the stomach should have been included with the intestine. The external opening, if such exists, is early closed, and if it is lost, as it may be, from the attached life of the young Amphiura, is probably always functionless. We have the following statement in regard to the anus of the young Amphiura. Apostolides states :† "Dans le stade suivant, où l'ébauche du tube digestif est complètement dessinée, on distingue bien au sommet de l'estomac, au milieu d'un bourrelet, l'orifice anal." This would seem to show that there is an anal opening, but how it is formed cannot be answered so far as observation goes at present.

In his first paper Metschnikoff recognizes an opening into the cavity of the larva, and considered it as formed by an infolding of the blastoderm. He was probably mistaken in supposing this opening to be the primary opening, or blastopore. He is believed to have missed altogether

* The abbreviation in development which leads to the reduction in the arms of the pluteus stage in Amphiura is not believed to cause any great modification or variation in the development of the primary plates of the test and arms. One or two writers have brought to their aid, in speaking of the apparent discrepancy in the time of the development of these plates in Amphiura and an Ophiuran with a pluteus, the possibility of modification by abbreviation in the former genus. The argument is deceptive, and should not be given too great weight.

† *Op. cit.*, p. 208.

the blastopore, and the gastrula cavity or future intestine, as he confesses practically in a later paper.*

The following quotation from Apostolides leads me to suspect that this author did not clearly distinguish the mesoblastic cells in his young Amphiura with a single cavity (intestine) and single opening (anus). Possibly he confounded them with the hypoblast. He says:† "Dans l'ectoderme on commence à apercevoir quelques points orangés premiers indices de calcification." If these calcifications are really formed in the ectoderm or epiblast, it is exceptional among larval Echinoderms, where they are regularly formed in the mesoblastic cells. Metschnikoff‡ rightly interprets the orange cells of the young Amphiura as mesoblastic or "cutis" cells. There is nothing in Apostolides' account either of Ophiothrix or of Amphiura to show that he recognized these cells which play such an important part in the growth of certain parts of the larval Echinoderm.

A study of Metschnikoff's Fig. 6. Pl. III.‡ is an instructive one. In this figure the epiblast (*ep*) is well formed, and the opening (an opening not figured, § but described in the text) on the lower pole is identified with the mouth opening of the older larvæ, which assume a bilaterally symmetrical contour. The young Amphiura is already bilaterally symmetrical, for on each side of the "opening" can be seen the beginning of the vaso-peritoneal vesicles, or water-tubes (*v*). At the pole opposite the supposed mouth there are trifid bodies (*cc*), identified as the provisional spines of the pluteus.

The homology of the parts of the larva mentioned has given me much trouble; for if we regard the so-called mouth as the original opening or future anus, the positions of the water-tubes and spines as compared with the same stage in other Echinoderms are wrong. If the opening in question (*mv*) is a mouth or second infolding of the epiblast, where are the intestine and the anus? In his admission* that Apostolides is right in his interpretation of the homology of intestine and anus Metschnikoff must have abandoned the idea that the interpretation of this figure is a correct one so far as the opening *mv* is concerned. I have found a larva similar to the figure quoted (Fig. 6), with the two transparent bodies (*v*) which

* *Zeit. f. Wiss. Zoöl.*, XXXVII. p. 307.

† *Op. cit.*, p. 210.

‡ Studien über die Entwickelung der Echinodermen und Nemertinen, *Mém. de l'Acad. Imp. des Sci. de St. Pétersb.*, VII^e sér. XIV. 8.

§ There is a mistake in lettering and in description. On p. 15 *mv* is spoken of as mouth. *mv* in the explanation of Figs. 3, 4, 5, is the vitelline membrane ("Dotterhaut").

he has interpreted as water-tubes, and I am led to regard it as admitting another interpretation from his. It shows that what he regards as mouth may be in reality the anus. I am not wholly settled in mind, however, in this conviction, especially if the two transparent bodies (*v*) are, as he interprets them, water-tubes, the right and left vaso-peritoneal vesicles. Their position would lead to the belief that Metschnikoff's interpretation is correct, for in all Echinoderms these bodies are found one on each side of the plutean or brachiolarian mouth. Subsequent larvæ, which are here figured, show that the provisional plutean appendages are not necessarily first formed at the anal pole, as these are situated in the larva he figures.

Mouth, Œsophagus. — The mouth (*or*) of Amphiura is formed by invagination. I was in doubt when I wrote my preliminary account of the development of Ophiopholis whether the primitive gastrula opening became mouth or anus of the pluteus. My figures* seem to indicate that the gastrula mouth becomes the plutean mouth; and if that is true, Ophiopholis is certainly exceptional. I find the same difficulty in the study of the development of Amphiura, although it seems as if the general law * of Echinoderm development ought to hold here as in Strongylocentrotus and others. In a bisymmetrical larva of Amphiura (Pl. II. Fig. 4) we have œsophagus, stomach, and intestine well developed. If there is in this

* *Op. cit.*, Pl. I. The law referred to is that the first opening, blastopore, is the future anus, and a second opening is found to develop into the pluteus mouth. This law has been found to hold in several genera of Echinoids, but has not been supported by observations of the Ophiurans. The supposition has been that in Ophiurans the law is the same as in Echinoids. Observations are now wanting to prove that such is the case. In my paper on the development of Ophiopholis it was not possible for me to prove that the gastrula mouth, blastopore, becomes the vent of the pluteus. The lettering *gm* (Pl. IV., *Bull. Mus. Comp. Zoöl.*, Vol. XII. No. 4) of the gastrulæ of Echinarachnius is a typographical error, as a reference to my text will show. In some other Echinoids the blastopore becomes the vent of the pluteus, according to most authorities. I have not observed the fate of the blastopore in Echinarachnius, and this erroneous lettering might imply that I was sure that the blastopore becomes the pluteus mouth. The candid reader of my text (pp. 128, 129) will I hope acquit me of holding that the blastopore becomes the pluteus mouth in Echinarachnius. Of the origin of the mouth of the pluteus it is said (p. 128): "The walls of this infolding" (second invagination) "break away and form the future anus (*v*) of the stages immediately following the gastrula, and probably the mouth of the pluteus." Of the fate of the blastopore in Echinarachnius I have no observations, and "nothing to show that there is any difference in this genus from what is recorded in Strongylocentrotus and other Echinoids" (p. 129).

larva an anal opening into the intestine, that opening would be functionally useless, for it is closed by the sac in which the embryo hangs. Before the young sever their attachment to the parent, anus and intestine are atrophied or highly modified so as to lose all semblance to these organs in other Echinoderm larvæ. The mouth also in very early stages, as can be observed by an examination of Figs. 5, 7, is closed by the sac in which the larva is suspended. It would not seem strange if, in the possibly abbreviated development which is found in Amphiura, a true anal opening never forms, and that the primitive gastrula cavity is formed not by invagination but by delamination. The intestine and anus in stages corresponding to Fig. 4 are not figured by Metschnikoff.

For a considerable time, and almost through the whole course of the development of the bilateral embryo, a conspicuous cluster of orange pigment is found at the anal pole of the larva near the intestine.

There are some difficulties in a comparison of the bilateral larvæ (Figs. 4–11) with others which have been figured by other observers. In the papers by Apostolides and Metschnikoff the position of figures of the same larva is different, and Metschnikoff does not follow in his figures the orientation given in the text. He says:* "Wenn man sich den Embryo mit dem Œsophagus nach oben, den Magen nach unten liegend denkt, so wird sich die Wassergefüsssystem Anlage auf der linken Seite befinden." This is a position exactly opposite that in which he has placed his figures. As the mouth on a median line is a convenient point for reference, its position ought to be mentioned when speaking of the position of the larva. When the mouth is turned to the observer and the anal end of the larva is above, the right water-tube (right-hand side of larva) is that which divides into five divisions. When the mouth is turned from the observer and the anal pole placed above, the left water-tube is that which divides to form the water-vascular system.

Umbilicus. — The connection of the bilateral larva with the ovary is by means of a structure which may be called the umbilicus, or "Nabelschnur" (*u*). It is at first, in young larval stages, broad and thick, and later becomes reduced in size to a simple string-like structure. Its existence prior to the pentagon-shaped larva is not indicated by Apostolides and Metschnikoff, although represented by Max Schultze. Metschnikoff† says: "Erst auf solchen Stadien (Fig. 17) könnte ich deutlich den von Krohn und Max Schultze bereits gesehenen Strang beobachten welcher sich dem das provisorische Skelet tragenden Körpertheile des Embryo inserirt." In the early conditions (Figs. 5, 8, 9) of the bisymmet-

* *Op. cit.*, p. 16. † *Op. cit.*, p. 18.

rical larva it is present, but has been ruptured in the young larvæ which he has figured prior to that represented in Fig. 17, and will be seen figured in my plate in some of these or corresponding stages.

Of the ultimate fate of the "Nabelschnur" (*u*) Metschnikoff says:* "Da er über schliesslich (ebenso wie das provisoriche Kalkskelet) verschwindert, ohne in den Körper des sich bildenden Sternes direct überzugehen, so muss man seine Rückbildung durch Atropie annehmen." That a part of the umbilicus and the whole of the provisional skeleton of the pluteus is absorbed seems to me true, as traces of the provisional skeleton (*ps*) are found in the pentagonal larva even when free from the mother. Of the freedom of the oldest stage when the remnant of the plutean skeleton was observed there may be doubt; but there can be little question that this skeleton enters into the formation of the future starfish, although possibly not directly into the formation of any special organ.

It is thought that all the "hunchback" part† of the larva figured in Fig. 7 passes by absorption into the embryo.

As to what part of the bisymmetrical larva is the homologue of the pluteus of Ophiopholis it may be said that the Amphiura young is a pluteus without arms, although the calcareous framework of the lateral arms is present. The larva (Fig. 7) is a pluteus with aborted arms.

Water-tubes and "Lateral Scheiben." — In the early stages of growth up to the pentagonal larva the water-tubes (Hydrocœlen) and the lateral bodies (Enterocœlen) were seen, but nothing new added to our knowledge of these structures. In one larva the right-hand water-tube is present after the left has begun to push out the five extensions which form the terminal tentacles. This tube was thought to open externally, and near its opening a trifid calcification was observed. It is known that monstrosities so called in the development of the tubes are said sometimes to give us a larva with even a pentamerous right water-tube, and it may be that this development belongs in this category. It does not seem reasonable that the right-water vesicle disappears, as stated by Metschnikoff.‡ We must wait in answer to the question of the fate of the right vesicle until we know the origin of the right "Scheibe," or enterocœl.

Observations upon the origin of the water-tubes of the Ophiurans are very much needed in the present state of science, and we can hardly put

* *Op. cit.*, p. 18.

† The protuberance on the right-hand upper corner of the figure imparts to the larva a hunchbacked appearance. All of this protuberance is absorbed in the growth of the young Amphiura.

‡ *Op. cit.*, p. 16.

great confidence in some of the speculations which have been indulged in until we know whether the Enterocœlen, and the Hydrocœlen or water-tubes, originate in Ophiurans as paired structures or not, and whether the right Enterocœl is the same as the right "Lateral Scheibe" of Metschnikoff or not. The question also of the connection of the water "tubes" with the oral plate or madreporite is also imperfectly answered. It may be supposed that the Hydrocœlen form from the Enterocœlen, which are themselves diverticula of the first invagination, and which persist in the form of the "Lateral Scheiben."

Provisional Spines of the Pluteus. — Max Schultze * first made the interesting discovery that the embryo of the viviparous *Amphiura squamata* is furnished with a provisional calcareous skeleton which is comparable with the spines of the arms of a pluteus. This important discovery has been verified by several observers. It presents us with a most interesting case of the retention of structures useful to free larva in an embryo where they can have no use, or if they have any use it must be a somewhat different function from that which they have in the free pluteus.

The provisional spines of the pluteus have a maximum development in the bisymmetrical larva (Fig. 8), but are not wanting in the younger stages of the pentagonal embryo, where they are very much reduced in size. The number, mode of origin, and position of the provisional spines of the pluteus seem to differ in different specimens. They are not always double or bisymmetrically arranged in reference to a plane passing through the mouth of the symmetrical larva and the umbilical connection with the parent. In the majority of instances the spine on the side opposite that in which lies the "left water-tube" is well developed, while that on the same side as the left water-tube is stunted (see Figs. 6, 7).

The provisional spines generally originate near the anal pole, but are found in some larvæ in the vicinity of the stomach and on one side of the body (Fig. 4, *ps*). In older stages of the bilateral larva the provisional spines form by reticulation a calcareous network (Fig. 10) similar to what we find in the anal lobe of Echinarachnius. This reticulation is hardly distinguishable from the permanent radial plates which form in the same position on the larva. The provisional calcareous rods are ultimately absorbed in the developing embryo, but do not wholly disappear until after the young Amphiura has passed into the pentagonal form (Fig. 13). When last observed they were noticed just under the region of the

* *Op. cit.*, pp. 44, 45; Pl. I. Figs. 2, 3, 4, 5 *a*. Krohn was not able to find a trace of the pluteus (*op. cit.*, p. 340).

body where the umbilicus is joined to the edge of the disk (Fig. 12). Metschnikoff has figured them in the same position in Fig. 17 of his Plate IV. There seems abundant evidence that they are absorbed into the body of the forming Ophiuran, as in Ophiothrix and Ophiopholis.

III. THE PENTAGONAL EMBRYO.

There are two forms or conditions in which the pentagonal embryo is found. The one (Fig. 12) of these follows in age close upon the bilateral larva, and is still attached to the mother; and the latter is represented by those larval stages when the young Amphiura has severed its connection with the parent and is leading an independent life (Fig. 13). The exact time at which the umbilicus is broken was not observed, but the rupture takes place certainly a relatively long time before the young leaves the parent. The young larva then seems for some time to live free in the parent without umbilical connection.

It becomes an interesting physiological question to determine the mode of alimentation of a young Amphiura in the body of the parent, and with no real connection with the adult. It would seem as if in older stages at least the young might be nourished by foreign matter taken into the open mouth. The genital slits of the parent would furnish an easy entrance for foreign bodies or small animals into the sacs, and the young Amphiuræ while free in the body of the parents probably use these bodies as food.

A. THE DISK.

1. Plates of the Abactinal Region of the Disk.

Dorsocentral and Radials. — The aboral integument of the disk has embedded in it in young stages of growth six reticulated calcareous plates. These plates consist of a single central, dorsocentral (*dc*), and five radials, the primary radials or radialia (*rp*). These plates have been observed, figured, or described by Krohn,* Schultze,† Lyman,‡ A. Agas-

* *Op. cit.*, p. 341. Krohn figures (Pl. XIV. Fig. 1) a cross-shaped dorsocentral surrounded by a continuous calcareous ring with no separate radials. This "einzigen Stücke bestehende Kalknetz" gives rise to "fünf Schuppen." The radials, according to a note on this page, are isolated from the beginning.

† *Op. cit.*, p. 41.

‡ Ophiuridæ and Astrophytidæ, Old and New, *Bull. Mus. Comp. Zoöl.*, Vol. III. No. 10, p. 264.

siz,* Metschnikoff,† and Ludwig.‡ The dorsocentral early takes its permanent place, and remains near the centre of the abactinal region of the disk; the radialia are subsequently to formation pushed nearer the periphery by the interposition of new plates between them and the dorsocentral. They are never, however, in Amphiura pressed to the very periphery of the body, and consequently never extend out on the arms. In early stages the dorsocentral § is not formed, the five radialia originating first.

The dorsocentral in the young Amphiura (Fig. 13) occupies the centre of the abactinal surface of the body, and is irregularly pentagonal. Its origin was not traced, but there is no reason to question the observations of Ludwig‡ and Schultze‖ that the radials appear before the dorsocentral. In the youngest pentagonal embryo which was studied (Fig. 12) in which the umbilicus (*u*) was still unbroken, the five radialia (*rp*) were well formed and of comparatively large size, while the dorsocentral (*dc*) was small, indicating apparently a later formation. Ludwig‡ says, "Ganz unterdrück aber wird die Entwickelung eines Centrale niemals." The radialia or primary radials are among the first plates to form, and originate while yet the Amphiura is in a bilaterally symmetrical condition. It is extremely difficult to distinguish them in earliest conditions from the network at the anal end of the provisional pluteus rods (Fig. 8), but they are among the first plates of the Amphiura to form. The question of whether they antedate in formation any of the plates of the actinal region of the disk will probably be correctly answered in the affirmative. They probably appear before the first pair of adambulacral (*q. v.*) plates and undoubtedly before the terminalia (*q. v.*).

A. Agassiz states:¶ "We have the most positive proof of the origin of the dorsocentral plate of starfishes and Ophiurans as a single Y-shaped rod appearing simultaneously with the five basals." Ludwig, on the other hand, states: "Diese sechste Platte, das Centrale tritt bei *Amphiura squamata* in der Regel später auf als die fünf Radialia." Ludwig holds**

* Embryology of Echinoderms, *Mem. Amer. Acad. Arts and Sci.*, III. 1856.

† *Op. cit.*, p. 18; Pl. IV. Fig. 17.

‡ *Op. cit.*, p. 195.

§ The reader is referred in this connection to Fig. 16, Pl. VII., in my paper on the development of Echinarachnius (*Bull. Mus. Comp. Zoöl.*, XII. 4). In this figure, which is of a young sea-urchin, the calcareous network of the dorsocentral plate (*c pl*) has not begun to form, although that of the ring of plates surrounding it is well marked.

‖ *Op. cit.*, Pl. I. Fig. 4.

¶ Report on the Echini, *Mem. Mus. Comp. Zoöl.*, Vol. X. No. 1.

** Page 187.

that the terminals appear at the same time as the radials, but could not determine whether their origin is earlier or later in time. He considers it probable that the terminals appear earlier. It is suggested that they appear in Amphiura* later, as their comparative sizes (shown in my figures) indicate. It is believed that Ludwig is right in his statement that the centrale (dorsocentral) appears later than the five primary radials in Amphiura.

It is interesting to see how far this order of late development of the dorsocentral is repeated in plates of the Asteroidea and Echinoidea supposed to correspond with the dorsocentral, radials, and terminals. Our knowledge of the sequence of the development of these plates is hardly accurate enough to make definite statements, but there seems to be some resemblance in these three groups in this particular.

According to A. Agassiz,† the abactinal system of the young Echinoid "consists of a single large plate, . . . and the new plates are added in a spiral manner round the anal plate." This large abactinal plate is figured in Fig. 28† and in several figures by Lovén. It would appear from this that they regard‡ the suranal plate as formed in sea-urchins of this age before the oculars and genitals. A. Agassiz finds in Salenia an adult genus with this plate, as in the young of some other genera; and according to Lovén,§ in this genus (Salenia) this plate is retained through life, and instead of being a temporary is a permanent structure. A. Agassiz‖ has examined specimens of young Saleniæ to obtain information in regard to the suranal plate and its homology with the "single large anal plate of the early stages of young Echini belonging to other families;" but he finds that "the arrangement of the plates of the abactinal system does not differ from that of the older specimens, the suranal being only pro-

* Sladen (*op. cit.*, p. 27) judges from the figures of larval Ophiurans which pass through a pluteus stage, given by Agassiz, Metschnikoff, and Müller, that it is more probable that traces of the terminal plates appear before the first radials. In the case of the Amphiura studied and figured by Metschnikoff, and possibly from the figures of Müller, he finds the reverse seems to occur. My observations on *A. squamata* show that the radials are well formed before the terminals attain any great size, or that the radials are of considerable size before the terminals have grown from a simple spicular form.

† Embryology of Echinoderms, *Mem. Amer. Acad.*, IX. 1864, p. 12, Fig. 28.

‡ Revision of the Echini, *Mem. Mus. Comp. Zoöl.*, p. 280, Pl. IX. Figs. 3, 6, 7, 8; Pl. X. Fig. 2.

§ Études sur les Échinoïdées, *Kongl. Svenska Vetenskaps Handlingar*, Bandet 11, No. 7.

‖ Report on the Echini, *Mem. Mus. Comp. Zoöl.*, Vol. X. No. 1.

portionally smaller." This fact has possibly a meaning in the comparative time when the suranal (dorsocentral) is formed, as compared with the ocular and genital, as will be spoken of directly.

In regard to Neumayr's statement that in the young "Glyphostomes" the anal plate is first formed, and that the plates of the genital ring are later detached from it, A. Agassiz* states that undoubtedly the anal plate in young Echinoids is the first plate to appear, and that genital and ocular plates are independently formed around it.

Our interest in the study of the dorsocentral plate of Amphiura is connected intimately with the origin of the suranal plate of the Echinoids. In Echinoids of some genera, according to the authority mentioned, the abactinal region is covered by a large single plate, suranal, which is possibly the dorsocentral, while in Amphiura a plate believed to be homologous, dorsocentral (*d*), is very small in young stages, and is thought to be developed *after* the radials. While opinions may be divided as to the homology of the primary radials in Amphiura with ocular and genitals of sea-urchins, it would seem as if a uniformity of opinion might be arrived at in regard to the dorsocentral. If, however, in Echinoids this plate forms before the ocular and genitals, and in Amphiura after the same, one is tempted to ask whether they are homologous. One might, of course, avoid the difficulty by the truism that the relative time of development is of little consequence, and that the appearance of the plate in Amphiura is simply retarded. Such an escape from the difficulty does not give much satisfaction, even if we remember the abbreviated development of Amphiura. The theory that the dorsocentral of Amphiura is homologous to the suranal of sea-urchins is believed to be true. As far as any objection based upon the different time of appearance of this structure is concerned, it is first necessary to examine the observations adduced in its support.† While the evidence seems to be against the late formation of the dorsocentral in Echinoids, the author is confident that in one genus of Echinoids, viz., Echinarachnius, no single plate centrally placed, which represents the suranal, is developed before plates regarded as homologous to the oculars and genitals. He believes that the suranal, which

* Report on the Echini, *Mem. Mus. Comp. Zoöl.*, Vol. X. No. 1, p. 33.

† It is believed that the difference in relative time of the appearance of the dorsocentral, and the ten plates around it, in Strongylocentrotus and Amphiura cannot be satisfactorily studied except from stages of the former genus much younger than those figured by Lovén for this purpose (*op. cit.*, Pl. XXI.). There is a call for a study of the young sea-urchin, between these and the pluteus, before we can definitely state whether dorsocentral or the ten surrounding plates first appear, or whether they appear simultaneously or not.

is here regarded as the dorsocentral, is developed after the oculars or genitals,* and that the dorsocentral is formed axially to the same. In Toxopneustes, according to authority mentioned, the facts seem to be diametrically opposite those mentioned for Echinarachnius, while the last-mentioned genus resembles Amphiura so far as the time of the development of the dorsocentral is concerned.

The dorsocentral of the starfish, Asteracanthion, is apparently formed in some cases after the radials (oculars) and genitals. In Asterina the dorsocentral seems to coexist with the other ten plates from the first, as shown in Ludwig's figures, although he does not say whether the dorsocentral appears before or after the other ten. Lovén's figure of the young *A. glacialis* (*op. cit.*) is not young enough to answer our question. In A. Agassiz's Embryology of Asteracanthion it is shown that the ten calcareous rods are the first to form, and attain a considerable size before the dorsocentral is represented. Metschnikoff gives very instructive stages † of the young of an unknown Asterid ; but his description is so short, and the arrangement of plates in it so remarkable, that it would be out of place to interpret them here. This stage and those preceding it give no answer to the question when the dorsocentral is formed. The question which plates in the young Amphiura correspond to the oculars of sea-urchins assumes a new phase in the light of what we know of the permanent retention of the radials in the abactinal hemisome of the body of Amphiura, and the relation of the terminals to the primitive tentacle. Now that we know that the primary radials of Amphiura are not pushed out to the extremity of the rays, but always remain in the disk, and that another

* Consult Pl. VII. Fig. 16, *Bull. Mus. Comp. Zoöl.*, Vol. XII. No. 4. This figure is thought to show the truth of the belief stated. No limestone rods were observed in *cpl*, which occupies the position of the suranal or dorsocentral.

† The figures alluded to are found on Pl. XII. Figs. 1 and 2 (Studien über die Entwickelung der Echinodermen und Nemertinen). Fig. 1 is an abactinal view, with five large peripheral, spiniferous plates, and a madreporic plate (*Mp*). Within this ring of peripheral plates are seven smaller, non-spiniferous plates, one of which is centrally placed. Metschnikoff was unable to determine the genus to which this starfish belongs. He found the absence of the anus to recall Astropecten, Luidia, or Ctenodiscus, but supposes that the character of the spines does not belong to these genera. With this objection, so far as the size and general arrangement of these huge spines are concerned, I cannot agree with him. I have studied the young of our *C. crispatus*, and find the five peripheral plates which he figures, each with three large conical spines, a median and two lateral, on each plate. Between each pair of these peripheral plates, which are regarded as the terminals, there are three adambulacral plates in each interradius, while in the stage figured by Metschnikoff there is but the single madreporite in this position.

set of plates (terminals) do suffer the change, we have this difficulty in a comparison of the young Echinoid with the young Amphiura. The terminals of Amphiura are independent centres of calcification from the radials. If terminals and radials in Amphiura lie in the same radius, how can the one or the other, especially the former, be the same as the oculars of the sea-urchin? If we compare the apical region of a sea-urchin and the abactinal hemisome of the young Amphiura, we have in Amphiura the terminals, plates which are supposed to be the same as oculars of the sea-urchins. If that is so, what plates in sea-urchins can be found to represent the radials of Amphiura, plates which are separate calcifications in both Ophiurans (Amphiura) and Asterina between terminals and dorsocentral? None exist. If, on the other hand, we say the oculars of sea-urchins are the homologues of the radials of Amphiura, they are not the same as another definite calcification, the terminals situated at the tip of the arm. Is it not more logical, from embryological grounds, if we compare the apical system of young Echinoids with the abactinal hemisome of Amphiura, not to suppose the first-formed plate in an ambulacral radius is an ocular homologous to a terminal, but an ocular homologous to a radial; provided, of course, we compare the radial series of Amphiura with the radial series of Echinoids?* Is it possible that what we call the ocular of the sea-urchin is in reality a consolidation of the radial and the terminal, or that a plate homologous to the radial is never developed? Either of these conditions would be a possibility, and more probable than that the eye-plate of the sea-urchin

* By the "radial series" of plates in Amphiura the author means the series which lies in the radius extending from the centre of the dorsocentral through the middle of the primary radials and terminals. By the radial series of the sea-urchins, the author means those plates which lie in a radius extending from the centre of the dorsocentral through the ocular. The above remarks in relation to radials and oculars of Ophiurans and sea-urchins apply to those who compare the terminals of starfishes and brittle stars without pluteus, with the ocular plates of the sea-urchin. Those, on the other hand, who compare the terminals and radials (primary) of Amphiura are believed to have this difficulty. If the terminal of Amphiura is compared with the genital of a sea-urchin, the madreporic opening of the Echinoid, which lies in the same interradius as a genital, ought to lie in the same radius as a terminal in Amphiura. The same objection would hold in a comparison of the radialia of Amphiura and the genitals of sea-urchins; the madreporic body, which in the young Amphiura is found in a plate called the oral, in the interradius would be found in the radius. This, of course, supposes the fact that the genitals and the madreporic body, since they lie in interradii, are comparable, and waives the homology of the so-called ambulacral plates, which Ludwig does not find in sea-urchins except in the auriculæ.

is homologous at the same time to the radials and the terminals which originate in both Amphiura and Asterina in two separate calcifications.

A comparison of the young sea-urchin with the young Amphiura reveals the following fact. The radials (*rp*) of Amphiura occupy a position, as regards the dorsocentral, similar to that which the ocular plates of the young sea-urchin hold to its anal plate, which is regarded as the dorsocentral. In the sea-urchin the ocular plate is perforated for the eye-spot. The eye has not been found in the radials of any Ophiuran. In one case the plate is an ocular, or eye-plate; in the other it has no eye. Nor is the eye known in the terminal in the Amphiura. Is a plate with an eye homologous to one without an eye? This of course opens the question whether the "eye" of the starfish and the "eye" of the Echinus are homologous. I believe an answer to this question can only be given by a histological study of the eye and its relation to the water-tube in Echinoids. A. Agassiz has shown the relationship of the eye-spot to the unpaired tentacle of Asteracanthion, and it remains to be seen whether in Echinoids the eye-spot is similarly formed. When it has been shown that the eye-spot of Echinoids is homologous to the eye-spot at the end of the arm of the starfish, it may be asserted that the terminal plate of the starfish is homologous to the ocular of the urchin. The adult form of the starfish and of Amphiura would imply that the terminal plate or the plate over the eye-spot of the starfish is homologous to the terminal plate of Amphiura, notwithstanding an eye-spot has not been described in any of the Ophiurans. If an association of the eye-spot with a plate means homology of those plates, the oculars of the urchins and the terminals of the starfishes (Ophiurans) are homologous; but if homologous, what plate in the young sea-urchin corresponds with the radial (*rp*) of Amphiura?

From a comparison of the young Amphiura with the young Echinoid it would seem as if a non-ocular (without pigment-spot) plate (*rp*) in the former occupies the same relative position to the dorsocentral as an oculated plate in the latter. Are they not then homologous? From a study of the adult Amphiura and the adult starfish it would seem that the plates (*tp*) at the tip of the ray adjacent in the latter to an eye-spot are homologous. If the terminal plate of the starfish with the eye-spot is homologous to the terminal of an Amphiura, and the plate with the eye-spot is homologous in starfishes and urchins, we are led to suppose the radials of Amphiura to be plates unrepresented in urchins. It seems more natural to compare radials in Amphiura with oculars in sea-urchins, notwithstanding the position of the eye-spot.

According to Balfour,* the central calcareous plate appears after the five radials and the five interradials. From this reference and the others already mentioned, it would appear that in the starfishes, as far as observed, the dorsocentral forms after radials and interradials. On account of a discrepancy in the observations of Thomson and Götte it is difficult to compare the centrodorsal of Crinoids with the dorsocentral of the Ophiuran. It would seem from Thomson's account as if the centrodorsal was a single plate originating after the basals, but Götte holds that the centrodorsal is formed of a number of at first independent rods which arise simultaneously with the basals.

The shape of each of the five radialia may be seen by a consultation of Figs. 13, 14. In the early condition of the plates the calcareous network consists of a somewhat coarse, open reticulation, over which grows a finer network connecting portions of the larger reticulation, and finely knitting the whole together. This second kind of network does not appear in figures of the primary radials and dorsocentral which have been given by others.

The primary radials, as shown by Ludwig, are not pushed out to the end of the rays, as is believed by many naturalists. They always remain on the abactinal hemisome of the body. It is therefore necessary to modify what Balfour says on page 564,* of the formation of the plates of Ophiurans, that "the *original* five radial plates remain as terminal segments of the adult rays." The original five radial plates are believed to be the primary radials of the abactinal hemisome in Amphiura, and are recognized in late stages on the body of the Ophiuran.

Oral Plates. — There are certain plates (Fig. 18 *o*) situated in the interradii, peripherally to the dorsal plates, or radialia at the very rim of the disk, which, although belonging to the actinal hemisome, must be mentioned here. They in point of fact originate on the abactinal hemisome, and by subsequent growth are carried to the actinal hemisome, forming the oral shields. Their position of origin only will be spoken of here, as a description of them will be given in an account of the plates of the month (*q. v.*).

The oral plates originate on the abactinal hemisome in the interradii on the outer margin of the disk. The first, or one of the first, of these to appear is perforated (Fig. 17 *o*), and according to Ludwig,† is a madreporite or oral plate bearing the madreporic opening (see oral plates).

Intermediate Plates. — Certain plates which are next to form on the

* Comparative Embryology (Second Edition), p. 559.

† *Op. cit.*, pp. 196, 197.

abactinal hemisome after the primary radials and dorsocentral, were given by Ludwig the name of intermediate plates. These plates immediately following the primary radials form in the interradii, and may therefore be called interradials or basals. In the line of the radii also there are new plates beginning to form, among which may be mentioned underbasals and radial shields. We shall first consider the basals and interradials.

Basals. — The first interradial plates form on the periphery of the abactinal hemisome on interradii between contiguous radialia. They are triangular in shape, and occupy a triangular interspace between adjoining primary radials. These plates are commonly confounded with the orals, which are forced to the actinal surface of the disk before the interradials arise. The first set of interradial plates may be known as the abaxial basals or first interradials. The next plates to form on the abactinal hemisome after the abaxial interradials are also interradials, and arise in the corners left between the dorsocentral and contiguous radialia. They arise as trifid or quadrifid calcareous spicules, and are five in number. They are not, however, synchronous in origin. Even in this stage, although two rings of interradials are formed, the radialia are not separated from the dorsocentral, and the surface of the abactinal hemisome is mostly made up of the "primary rosette" of plates, the dorsocentral and the radialia. As the growth of the new interradial plates proceeds, the increase in size of the radialia and dorsocentral is not the same as that of the interradials, and the original rosette is more or less contorted in its form. Almost simultaneously with this contortion appear a number of plates, among which may be mentioned a new ring of interradials, five radial plates between the dorsocentral and the radialia, and the radial shields. In the formation of new rings of interradials, at least in the next set of plates, the newly formed seem to lie adaxially to those already developed. The next ring of interradials arises between the last-formed interradials and the periphery of the dorsocentral.

In the case of the radial series of plates, however, the next plates to form after the radialia are the radial shields. These plates are remarkable in more than one way. Anatomically they can be recognized in all genera of Ophiurans, and their mode of development in pairs is exceptional among radial plates of the disk. All abaxial plates thus far formed on the abactinal hemisome have originated singly, one in each interradius, and are five in number. The primary radials and basals follow the same law as far as the number five goes. The radial shields are the first in the abactinal hemisome to originate in pairs. On the actinal side we shall find all plates originate in pairs except the *tori*, or jaw-plates; but on

the abactinal side of the disk the plates which ultimately form radial shields are the first bodies to arise in this way. The radial shields lie just abaxially to the radialia, one on each side of a radius. In one instance, and that in the preparation figured, a median radial plate abaxially placed to the radialia had formed before the radial shields began to appear. In other specimens that was not observed to be the normal method of formation. I have figured this specimen from its similarity to a larva figured by Lyman,* about which more will be said later when considering the homology of the radial shields. It is not until the radial shields have reached some size that a radial plate is formed between each of the radialia and the dorsocentral on the lines of the radii. This last-mentioned plate, the underbasal,† tends to separate the primary radialia and dorsocentral, and from the first their edges do not join each other.

The interpolation of new plates in the abactinal hemisome now becomes more or less irregular. If any law for the formation of these plates exists, the modification in size of the plates renders it extremely difficult to trace it in their formation at this time.

The nomenclature of the intermediate plates on the abactinal hemisome is similar to that given by P. H. Carpenter in his discussion of Crinoidal and Ophiuran morphology.‡ It seems to me, however, that it would have been better, in considering the relationship of the basals in the young Amphiura and their homologues in the projection of the calyx of an Antedon larva, for Carpenter to have introduced, instead of his Fig. II. (a copy of one of Ludwig's figures), a copy of another (Fig. 25) of the same author. In this figure (Fig. 25) there is but one circle of interradial, intermediate plates and no "underbasals," while the intermediate plates of Ludwig's Fig. 25 and Carpenter's diagram of the Antedon (Fig. III.) numerically correspond. The additional intermediate plates, both radial ("underbasals") and interradial ("basals"), in the figure by Ludwig, which he (Carpenter) has chosen for Fig. II., lead to a difficulty in one particular in a comparison of the young Amphiura and Antedon. It is an important thing to know whether the intermediate plates of Ludwig's Fig. 25 are the same as the Plates 3 of Carpenter's diagram (*loc. cit.*, Fig. II.).

* Challenger Ophiuroidea, Pl. XL. Fig. 11, p. 157.

† Notes on Echinoderm Morphology, No. V. On the Homology of the Apical System, with some Remarks upon the Blood-vessels. *Quart. Journ. Micros. Sci.*, Vol. XXII. The homology of this plate with the Crinoidal underbasal is recognized by Carpenter.

‡ Notes on Echinoderm Morphology, No. V. pp. 10, 11. *Quart. Journ. Micros. Sci.*, Vol. XX.

This question can be answered in part by a knowledge of whether the ring of interradials just abaxially or outside of the so-called basals (3) are earlier or later in formation than the basals (3). They appear to be later, for in Ludwig's Fig. 21 we have a single interradial plate just beginning to form between an abaxial and an adaxial interradial (the abaxial is probably the oral). Moreover, this seems to be the mode of formation referred to by Ludwig in the words, "Es scheiben überall im Bereiche des dorsalen Scheibenperisoms neue Intermediarplatten zwischen und neben den einmal gebildeten sich anlegen zu können." If the intermediate plates are formed later, the Plate 3 in Carpenter's Fig. II. would be the same as one of the ring of interradials in Ludwig's Fig. 25, which exactly corresponds with the basals (3) of the projection of the Antedon larva.

The determination of the relative length of the arm when the underbasals and basals appear may be made by considering the relative development and number of pairs of the adambulacral plates. Carpenter states:* "The radials of the young Amphiura do not long remain in contact with the dorsocentral; for by the time that *two* adambulacral plates have appeared between them and the terminals they are separated from the dorsocentral by the rudimentary basal plates, while underbasals are developed shortly after." In the figure quoted (Pl. I. Fig. 12) by Carpenter in this connection, which is probably a little older than one necessary to illustrate the above statement, three *pairs* of side arm-plates (adambulacral) are figured between the terminal (*T*) and the primary radials (4). Two pairs of lateral arm-plates at least are developed before the plates which Carpenter calls basals appear. It is taken for granted that the lateral arm-plates are considered adambulacral by Carpenter, — a homology of which there is little doubt, — and must be the ones referred to by him, since they are the only plates, in the figure quoted by him (Pl. I. Fig. 12), between the terminals (*T*) and radialia (4).†

The homology of the radial shields of the Amphiura with the first brachials of the Crinoid would seem not unreasonable.‡ The only paired plates of the arms with which they could be compared are the adambulacral. With these, however, they have little resemblance save in their double origin.

* On the Apical System of the Ophiurids, *Quart. Journ. Micros. Sci.*, Vol. XXIV., Jan., 1884, p. 6.

† The first and second adambulacrals lie on the oral side of the disk, and cannot be those referred to by Carpenter as appearing *between* the terminals and radials.

‡ This suggestion is believed to be original, although it is a direct sequence of the adoption of the theory that the radials of Amphiura and of the Crinoids are homologous, as shown above (adopted from Carpenter and others).

Lyman * gives two very instructive figures of the young *Hemipholis cordifera*, from which he draws the following conclusion: "It thus appears that radial shields so nearly universal among Ophiurans are not special plates, but entirely homologous with other disk-scales, and by no means the first to appear." In the younger of these two stages of the young Hemipholis there is a dorsocentral surrounded by five radial plates and an outer circle of five interradial, while there are ten arm-joints. The development of the basal plates must be very much more retarded in this genus than in Amphiura; for in the latter, with half the number of arm-joints and many more interradial plates, the radial shields and some other plates have appeared. The second figure (Fig. 11, *op. cit.*) of a young Hemipholis older than the last is very interesting. In it there is a dorsocentral surrounded by five radials. In each of the interradii there are three interradial plates. There is a second radial beyond, abaxially to the primary radial. Peripherally placed to the second radial are radial shields, one on each side of the radius. The condition here is about the same as that which we find in an Amphiura in which the development of the arms is very much less (Fig. 19) than in Hemipholis. Every observation would probably agree with the above-quoted statement of Lyman, that the radial shields are not the first to appear; and it is thought that they are the same in mode of origin as the dorsocentral, radialia, or interradial plates. The radial shields arise before the underbasals, which are the only other plates in the radii in this early condition. They are the first of the radial series to arise abaxially to the radialia.

2. Plates of the Actinal Region of the Disk.

The plates of the mouth originate early in the development of the young Amphiura. The so-called V-shaped plates (ad^1, ad^2), described below as the first and second pair of adambulacral, are among the first to form, and can be seen as trifid calcareous bodies in the bilaterally symmetrical embryo (Figs. 7, 8, 10). Although I have not directly fol-

* Report on Challenger Ophiuroidea, Pl. XL. Figs. 11, 12, p. 157. As stated elsewhere, the young Ophiurans clinging to the arms of Hemipholis (Ophiolepis) were observed by Stimpson many years ago.

The younger stages in the formation of the plates in the young Hemipholis would offer an interesting subject for investigation for those naturalists who work in localities where it is found, as from a comparison of Lyman's figures of the young with those here given of Amphiura it is suspected that there is considerable variation in the two genera in this particular.

lowed them back to this larva, from a study of my figures and a comparison with Metschnikoff's Fig. 16, there seems abundant evidence that they precede all other plates of the actinal region of the disk. There is also evidence that they antedate the formation of the terminals, although they are probably formed after the radialia or primary radials.

Metschnikoff,* in speaking of the plates of the actinal region, says that the five parts of the skeleton on the ventral surface of the embryo represent the future jaws. Apostolides† also describes five V-shaped plates. There are really five *pairs* of these plates in early stages, and ten pairs in later conditions when both pairs of adambulacral plates are developed.

The following plates will be considered in our discussion of the mouth skeleton :

1. Adambulacral ; first and second pairs, ad^1 and ad^2.
2. "Ambulacral;" spoon-shaped plates, *os*, *spl.*
3. Oral ; mouth-shield ; madreporite, *o.*
4. *Torus angularis ;* jaw-plates, *to.*
5. Teeth, *t.*

Adambulacral Plates. — There are two pairs of adambulacral to be considered in this connection, known after Ludwig as the first (ad^1) and second (ad^2) pairs. They are both regarded as homologous to the side plates (*lp*) of the arms, which will be later described. The adambulacrals originate in pairs, five in number. The first pair (ad^1) support the *torus* (*to*). Both pairs are early formed in the development of the actinal hemisome.

First Pair of Adambulacral Plates. — The double origin of the "V-shaped" plates has been shown by Ludwig, and is evident from the figures of Max Schultze (Figs. 5, 6) and Metschnikoff. Apostolides † writes : "Les premières grandes plaques calcaires qui apparaissent avant même que le bras soit à peine ébauché sont les *cinq* pièces fourchues de l'adulte ; il est facile de se convaincre de leur apparition primitive, grâce à leur forme en V et la disposition des tentacules buccaux que

* *Op. cit.*, p. 18. The lettering *cc*, in Metschnikoff's Figs. 11, 12, 13, 16, and 17, Pl. IV., does not refer to the same structures as *cc* in Fig. 6, Pl. III. *cc* in Fig. 16 is an adambulacral plate ; in Figs. 11, 12, 13, and 17, it is a terminal, and in Fig. 6, Pl. III., it is one of the provisional pluteus plates. The rods *cc*, in Metschnikoff's Pl. IV. Fig. 16, are probably the first and second adambulacral. The following corrections may be made in "Selections from Embryological Monographs, Echinodermata" (*Mem. Mus. Comp. Zoöl.*, Vol. IX. No. 3, Pl. III.): *cc*, Figs. 9, 10, 11, and 14 are probably terminals ; in Fig. 13, *cc* are adambulacral, and not provisional limestone rods homologues of the pluteus rods.

† *Op. cit.*, p. 213.

nous avons mentionnée." On page 132 he writes: "On admet que ces pièces fourchues sont formées par la division d'un ossicule discoïde sur la ligne médiane, et la déviation de chacune des deux moitiés, jusqu'à la rencontre de la moitié correspondante du disque voisin à laquelle elle se soude." In these descriptions it seems probable that Apostolides refers to the first pair of adambulacral and possibly the second pair also. It can hardly be supposed that he refers to the first pair of ambulacral, which are later described by me as the spoon-shaped plates after Ludwig, since these never have a V-shape. Whether he refers in his description to the first ambulacral or the first adambulacral (with the second), it may be borne in mind that neither has been formed by a division of a "discoid" ossicle, nor are they ever five in number. The members of the five *pairs* of adambulacral as well as of ambulacral originate as ten separate calcifications. In the youngest condition (a stage a little younger than Fig. 17) of the growth in which they were observed the first pair of adambulacral plates were formed although the terminals were very small. I am therefore led to suppose that the first pair of adambulacrals appear before the terminals. In this embryo (Fig. 17) the pentagonal form is but obscurely indicated. The first pair of adambulacral are portions of the "maxillæ" of Metschnikoff's figure (Pl. IV. Fig. 18, *cc*).

The first adambulacral plates originate in pairs about the mouth (Fig. 15). In early conditions they lie more in those axes which later become the interradials, although they arise before the young has passed into conditions in which either radii or interradii can be definitely recognized. In Ludwig's Fig. 23 they are smaller than the terminals, but in some of my preparations they are larger.

In a later stage (Fig. 17), in which the rays have begun to push out, the first pair of adambulacrals assume a more or less irregular crescentic form, with concave edges turned to the radii. By a continued growth the adradial edge of these plates begins to approximate so that plates of adjacent pairs approach each other. This approximation is confined to about half their interradial border. The adradial half of the rude crescent extends to the mouth opening. By the approach of two of these first adambulacral plates (ad^1) which lie in different pairs, a V-shape is given to the combination. The plates however are free along the line of the interradii. The double network of these plates appears as in the radialia (Fig. 18, *rp*).

Of the homology of these plates with the adambulacral there seems no doubt. I believe also that Ludwig's comparison of them to the side

plates of the arms is a correct one, and borne out by their mode of formation as compared with the first ventral plate of the arms, as will be explained in a subsequent explanation of the formation of the ventral plates.

Second Pair of Adambulacral Plates. — The second pair of adambulacrals (ad^2) arise after the first pair, aborally to the same, and are situated more on the interradius than the first pair. These plates also differ from the first pair in the possession of appendages in the form of club-shaped spines. These spines are free at one extremity. The fact that the second pair of adambulacral plates as well as the side plates of the arms have spines would incline one to believe that they are homologous to each other. The second adambulacral plates are ten in number, in five pairs, and with the first adambulacral are among the earliest plates to form.

In Fig. 17 there will be seen between each pair of terminal plates (*tp*), on the periphery of the disk, two knob-like structures which extend beyond the edge of the disk. These did not escape the attention of Max Schultze,* who described them as extending beyond the disk as "keulenförmige Fortsätze." Ludwig† has also described these bodies, and recognized their resemblance to spines. They were purposely omitted by him from his figures. I think this omission is unfortunate, as they confirm a theory of the relationship of the second adambulacral plates which Ludwig supports, that these plates are homologous to the side plates of the arms. He says:‡ "Bezüglich der Homologie der Seitenplatten am Arme der Ophiuren mit den Adambulacralstücken der Seesterne kann ich auf meine früheren Ausführungen verweisen und brauche wohl kaum zu bemerken, dass diese Homologie auch in den eben erwähnten entwickelungsgeschichtlichen Thatsachen eine Stütze findet." The position of the second pair of adambulacrals so called, and the club-shaped appendage seem to refer these plates to the same category as the side plates of the arms, and make them homologous with adambulacral plates elsewhere among stellate Echinoderms.

The club-shaped appendages lose their relatively large size as the growth of the arm goes on, and it is only when the terminals are just beginning to be pressed out from under the radialia that their projection beyond the edge of the disk is noticed. These club-shaped spines can be seen by looking at the young Amphiura from the abactinal as well as the actinal regions.

Ambulacral Plates. — Of the plates which have been referred to the

* *Op. cit.*, Pl. I. Fig. 5 *c*, Fig. 6 *d*, p. 42.

† *Op. cit.*, p. 194.

‡ *Op. cit.*, p. 189.

ambulacral series, there are two pairs which may be considered in the account of the plates of the actinal region of the disk of the young Amphiura. The former of these, or the adoral pair, are known as the spoon-formed plates (*spl*); while the second, partially concealed from view in some of my figures, form the ossicles which complete the calcareous ring of the mouth. The spoon-shaped plates may be known (following Ludwig) as the first pair of ambulacral; the second as the second pair of ambulacral. The former are superficial in their position; the latter more profound. Both resemble each other in their paired origin.

Spoon-shaped Plates. — If we study a young Amphiura in which the pentagonal form has been donned (Fig. 15), there will be noticed in the radius near the mouth opening and between adjacent pairs of first adambulacral plates two elongated reticulated plates placed side by side. These plates are commonly pointed on the adoral ends, more spatulate at the other extremities. They originate early in the growth of the embryo, and in young stages are equal in size to the first pair of adambulacral. The increase by growth of the first pair of adambulacral plates leaves, however, the spoon-shaped plates smaller than the adambulacral. Their position leads to the theory that they belong to the ambulacral series, and their mode of origin does not disprove what their position teaches; but it may be doubted from their want of connection with the first pair of adambulacral plates in early conditions (*vide infra*) whether they are "ambulacral plates."

Second Pair of Ambulacral Plates. — The aboral radial ends of the first pair of adambulacral plates of adjacent pairs of these structures are knit together by two plates which are classed as the second pair of ambulacral plates. These plates form the radial part of the circumoral calcareous ring, and occupy the same position as regards the first pair of adambulacral plates as the arm-joints do to the side plates of the arms.

That the second pair of ambulacral plates are ambulacral in their homology is not doubted, but the fact of their union with the first pair of adambulacral has led me to doubt whether they were not the *first* pair of ambulacral instead of the second. There seems much to support this theory, for it brings all the ambulacral plates whether of the disk or arms into harmony; viz., an ambulacral plate is joined to a corresponding adambulacral. The spoon-shaped plates not only show an exception in their superficial position, but also in early condition are not joined to the first pair of adambulacrals. Although for convenience they are in this paper designated as the second pair of ambulacral plates, it is not wholly clear to me that they are not in reality the *first* pair, and that

the spoon-shaped plates are not ambulacral. If the spoon-shaped plates are ambulacral, they are highly modified.

The manner of growth of the ambulacral plates has been carefully described and figured by Ludwig, and I have little to add to his account.

They originate in pairs one on each side of the median line of the arm in a deeper region of the arm on the ventral side. In their earliest form they appear as trifid spicules or small parallel bars. These two members of a single joint unite over the median line, forming by coalescence the solid arm-joint. The union of the separate calcifications has been well figured by Ludwig. The union takes place at first on the adoral and aboral ends, so that in a half-formed arm-joint a median unclosed opening remains after the junction of the two ends. The body thus formed is at first much longer than broad ; later it becomes discoid, when the consolidation is complete.

The distinction between ambulacral and lateral arm-plates is recognizable from very early conditions, and the former are well consolidated before union with the lateral plates is effected.

That the ambulacral plates of Ophiurans are spurs of the side plates was questioned by Lyman,* from his study of certain lower genera of deep-sea Ophiurans, Ophiothelia and Ophiohelus. The separation of the two members which compose one of these "arm-bones" even close to the tip of the arm affords a difficulty in accepting the theory of some naturalists that they originally formed as spurs from the small lateral plates. The development of the plates in Amphiura shows that the arm-joints, "ambulacra," and lateral arm-plates not only originate in two separate calcifications, but also that they have great similarity to the permanent plates in such a genus as Ophiohelus. Attention has been called by Ludwig to the resemblance of the unconsolidated ambulacral plates of Amphiura and the same plates of the deep-sea Ophiuran Ophiohelus. Lyman first suggested the embryonic nature of the unjoined arm-joints of Ophiohelus and other genera.

Orals, or Oral Shields. — The position of the first-formed orals (*o*) is an interesting one ; and a morphological interpretation of their relationship to plates in other Echinoderms is beset with many difficulties, which others have discussed.†

* A Structural Feature hitherto Unknown among Echinodermata, *Ann. Mem. Bost. Soc. Nat. Hist.*, 1880, pp. 3–7, Pl. I. Fig. 12. Report on the Ophiuroidea dredged by H. M. S. Challenger during the years 1873–76, Zoölogy, Vol. V. pp. 237, 238, Pl. XXVIII. Fig. 6.

† Ludwig, Ueber den primären Steinkanal der Crinoideen, nebst vergleichend-

The orals originate near the margin of the pentagonal larva, and have a part of their extent at least on the abactinal side. A single oral which is pierced by an opening is larger than the rest, and is one of the first to form. This is supposed to be the same as the madreporic plate. It is larger than the remaining orals, and like them, by the increase of the plates in the interradii between them and the dorsocentral, is forced in the growth of the disk to the actinal side of the body. In their youngest condition the orals resemble other plates in their spicule-like shape.

The literature written by those who have observed the development of the plates of Amphiura does not agree with Sladen when he says:* "The orals and some of the accompanying plates of the actinal hemisome next appear [after radials and terminals] before any trace of the dorsocentral plate is present." If he means that all the orals appear before the dorsocentral, it cannot have been knowledge derived from what has been published on the development of Amphiura; for Ludwig has said nothing to support such a statement, nor does his figure show more than one oral before the formation of the dorsocentral. On the other hand, Krohn in 1851 and Metschnikoff † eighteen years after figure a well-developed dorsocentral plate before any sign of an oral. It will not be claimed that the figures of the last-mentioned naturalists are perfectly accurate in this particular, for it is believed that the madreporic plate ought to have been represented by them in figures showing the immature dorsocentral, but one cannot suppose that they support Sladen's statement. In Ludwig's Figs. 17, 23, in which no dorsocentral exists, the madreporic plate is formed, but there is no other oral represented. In his Fig. 19, where the dorsocentral is well developed, one of the orals is little more than a three-pronged spicule. Evidently here the dorsocentral has antedated in formation one of the orals. My preparations teach me that the dorsocentral is of considerable size before some of the orals.‡

anatomischen Bemerkungen über die Echinodermen überhaupt, *Zeit. f. Wiss. Zoöl.*, XXXIV. pp. 318–322. Neue Beiträge zur Anatomie der Ophiuren, *Zeit. f. Wiss. Zoöl.*, XXXIV. p. 342. Entwickelungsgeschichte der Asterina gibbosa, *Zeit. f. Wiss. Zoöl.*, XXXVII. Carpenter, *Quart. Journ. Micros. Sci.* XX. (*ns*).

* *Op. cit.*, p. 29. † *Op. cit.*, Pl. III. Fig. 17.

‡ What is said above is on the supposition that Sladen calls the orals the plates (5, Pl. I. Fig. 13), and no others. I think I am just in this supposition. If however he includes among orals the spoon-shaped plates and the adambulacral, as might be done, my criticism above would be unjust, and I gladly withdraw it.

Sladen's paper on the "Primary Larval Plates of Brachiate Echinoderms" devotes some space to the homologies of the odontophore of the starfish. As he does not consider in this discussion the first pair of adambulacral and the spoon-shaped plates

Torus angularis and Teeth. — These structures arise later than the first pair of adambulacral plates, but develop quite early in the growth of the young Amphiura. They form as independent calcifications. The torus is at first an elongated plate or bar, which later becomes semicircular. In Fig. 20 this plate is represented as perforated and reticulated. It appears that the teeth are not separate centres of calcification, but grow out directly from the adoral region of the torus. The calcareous deposit which enters into their formation has the form at first of a reticulated perforated triangular plate.

B. PLATES OF THE ARMS.

The plates of the arms are the following: —

1. Terminals, *tp*.
2. Side plates, *lp*.
3. Ventrals, *v*.
4. Dorsals, *d*.

Terminals. — The terminal plates (*tp*) which lie at the aboral extremity of the arms have been described by many observers. These plates have been confounded by many writers with the radials. Ludwig * first distinguished them from what are already described as the radialia or primary radials. The fact that certain plates early formed in the young Ophiuran were pushed out by a growth of new plates was known, but in all cases these plates were regarded as "primary" plates and were in some instances morphologically misinterpreted. In Amphiura Krohn † has figured the terminal plate, but gives it no special description. Max Schultze ‡ recognized the fact that the terminals belong to the arm proper, and correctly designates them as the "erste Anlage der Arme." A. Agassiz § observed the terminal plates in an Ophiuran, probably Ophiopholis, which he referred to Amphiura. He regards them as the first

of Amphiura, it might be supposed that he does not consider these early formed plates as primary plates of the *test*. In strict language they are mouth-plates, but are so early formed in the larva that they may be regarded as primary plates. As a question of opinion I think they ought to be mentioned in a discussion of the homology of the odontophore.

* *Op. cit.*, p. 187.

† *Op. cit.*, Pl. XIV. Fig. 1, *b*; p. 342.

‡ *Op. cit.*, Pl. I. Figs. 4, 5, *c*. In Fig. 6 they are lettered *f*. He does not seem to have connected Plate *c*, Figs. 4, 5, with *f*, Fig. 6.

§ *Op. cit.*, p. 20, Fig. 32, *y*.

developed dorsal shields (primary radials?). Ludwig* regards this interpretation as incorrect. A. Agassiz has shown that this plate is forced out by growth of the arm to its distal extremity. Metschnikoff† correctly figures the terminalia, and regards them as the "ersten Anlage der Wirbelstücke." The true arm-joints or ambulacral plates, which are regarded the same as the "Wirbelstücke," are formed as a rule in pairs, not medially and unpaired. Ludwig‡ gives an accurate account of the growth of the terminal plates, and shows that they form early in the career of the young Amphiura. He is doubtful whether they originate before or after the radialia, and regards it as probable that they are formed *before* the radialia or primary radials. Carpenter and Sladen§ have discussed the homologies of the terminalia, adding no new facts, but drawing for illustration from the excellent paper of Ludwig so far as the development in this genus Amphiura is concerned. Sladen§ says: "The primitive structure and mode of formation of the terminal plate is different from that of the first radial." It seems to me that the difference in primitive structure, if any, ought to have been more fully pointed out, and it is doubted whether there is any great difference in these particulars. I find nothing in Ludwig's account to justify the above statement of Sladen, and my own observations show that both the terminal plate and the first radial have many points of resemblance in "primitive structure" and "mode of formation." It is not intended to be denied that the form of the terminals and first radials may differ from the very first, or that they cannot be distinguished one from the other.

The terminals originate *after* the primary radials. This statement, hardly in accord with that of Ludwig, is supported by the figures of Krohn, Schultze, and Metschnikoff,† in which the terminals are much smaller than the radials, and in which the indications are that the latter are just forming. My own observations support the statement. I have never, however, recognized a young Amphiura with radials and without terminals. The terminal plate originates on the abactinal side of the water-tube, or "feeler," and by a growth of the arm is pushed out to the very end of the ray (Fig. 12). According to Lyman,|| the terminal plate is a hollow tube; and according to Ludwig,* it grows from the abactinal side around the feeler on both sides, joining on the actinal side. The

* *Op. cit.*, p. 187.

† *Op. cit.*, Pl. IV. Fig. 17.

‡ *Op. cit.*, pp. 187, 188.

§ *Op. cit.*, pp. 29, 30.

|| Ophiuridæ and Astrophytidæ, Old and New, *Bull. Mus. Comp. Zoöl.*, Vol. III. No. 10, p. 258, Pl. V. Figs. 1, 2, 3, 4.

end of the water-tube is said by him to pass through the tube thus formed.

The significance of the terminal plate has played an important part in discussions of Echinoderm morphology, and is by many thought to be the same as the ocular plate of the starfish. This opinion seems well supported; but whether the terminal or the radial is the homologue of the ocular of the sea-urchin is open to discussion.

As to the exact relationship of the terminal plate to other plates of the arm, it may be well to inquire whether it cannot be homologized with the so-called dorsal plate of the first or second adambulacral plates of the actinal region of the disk. That question will be considered, not answered, in our discussion of the dorsal plates of the arms.

When the arm is broken, a new terminal is formed by being pressed out by the growth of new plates, just as in the originally formed terminal plate. In the very instructive figures of the young of *Asterias glacialis*, Linn., by Lovén,* we have (Fig. 257) in the radial plate (*p*) a structure which may be considered the primary radial. If, however, we regard *p* as homologous to the radial plate, *rp*, of the Amphiura young, as its position on the radius would seem to indicate, its time of development, as compared with the interradials, *b*, is much retarded. It seems, indeed, not improbable that *p*, Fig. 257 (Lovén, *op. cit.*), is one of the series of plates along the middle aboral line of the ray, three of which are shown in Fig. 259. Possibly these plates are homologous with the dorsals of Amphiura and other Ophiurans. Lovén's figures (Figs. 256, 258) are interesting in another way. In the former of these, which is a view from the actinal side, in each interradius, there are two plates which in Fig. 258 bear spines. What are these plates? No one seems to have asked the question, as it is perhaps thought to be self-evident that they are adambulacral. As compared with the young Amphiura they have similarities with the second pair of adambulacral (ad^2). As in Amphiura these plates, although homologous to the lateral plates, are somewhat modified, so in the young *A. glacialis* they are somewhat different from other adambulacral plates. Among all the plates of the arm the terminal offers this peculiarity. It is the only plate which originates on the dorsal side of the water-tube and grows around it to the ventral. It therefore originates like a dorsal, and when grown occupies also the position of both laterals and possibly the ventral. Is it homo-

* Études sur les Échinoïdées, *Kongl. Svenska Vetenskaps Handlingar*, Bandet 11, No. 7. The plate *p*, according to Lovén, is a plate of the "système périsomatique." In the very young there is a single median series in this species.

logous to the other plates of the arms, and if so, to which, — dorsals or laterals or ventrals? In its mode of origin it is very much like a dorsal. It arises in the median dorsal line; it is single. It grows on the sides of the vessel as a lateral. With the ventral it has no resemblance. If it were possible to carry the homology of plates so far that every pair of adambulacral plates should have corresponding dorsals, it would be necessary to regard the primary radials as the dorsals of the first pair of radials, and then the terminals might be regarded as the dorsals of the second pair of adambulacrals. The third pair of adambulacrals would then be represented by true lateral plates, with a dorsal in the arm itself. This supposition and all similar theories seem to be overthrown by the fact that the terminal in the growth of the arm is pushed to its tip, far away from the plates with which it occupies relationships in early life. Whether it will be found that the terminal is a modified dorsal or lateral plate, or a plate unrepresented in other regions of the arm and disk, its fate in the formation of the arm is unique. While its early structure as a spicular calcification on the median radius resembles the radialia and the dorsal plates, its form in the adult is very different from these structures, and its relations to the water-vessel such as no other plate of disk or arms has.

Side Plates. — The side plates (*lp*) of the arms are regarded as adambulacral in their homology. They originate laterally and in pairs, growing dorsally and ventrally until they approximate dorsals and ventrals. The oldest side plates are adoral, and new side plates form between those already present and the terminals. The first pair of side plates originate *after* the *first ventral* (*V*), and before the arm has begun to push out. They therefore appear when first formed in the wall of the disk. Spines arise from the aboral edge of the side plates, those on the first pair of side plates being well formed before the fourth pair of side plates have appeared (Fig. 20). The time of the appearance of the side plates as compared with the first ventral will be seen, by a comparison of the above statement with that of Ludwig, to be contradictory. Ludwig says:* "Es entstehen aber die zu einem Armgliede gehörigen Seiten-Dorsal- und Ventralplatten nicht etwa auf einmal sondern zuerst sich nur die Seitenplatten an." While both *V* and V^1 (Pl. XI. Fig. 18, *op. cit.*) are regarded by him as ventral, especial attention is turned by Ludwig to V^1 as the first ventral, in his reference to the sequence of the formation of the side plates and ventrals. I believe that the contradiction pointed out between Ludwig's account of the sequence of these plates and my own is apparent

* *Op. cit.*, pp. 188, 189.

rather than real; for the ventral plate *V* belongs to the first pair of adambulacral plates (ad^1), which are themselves homologous with side plates. Although the first ventral (*V*) is formed before the first side plates, it appears after the first adambulacral pair to which it belongs. Considering these facts, the law pointed out by Ludwig,* that the side plates precede the ventral in time of formation, holds likewise for the first adambulacral, and is true of the side plates if we give them their true interpretation as adambulacral plates.

Ventral Plates. — The ventral arm-plate or under arm-plate is early developed in the young Amphiura. The first ventral (*V*) is already well formed when the terminal plate has just begun to push its way axially from the periphery of the disk. The first ventral plate (Figs. 16, 17) is formed before the first side plates of the arm, but after the first adambulacral. Ludwig* states: "Erst nachdem die Seitenplatten sich angelegt haben, beginnen auch die Dorsal- und Ventralplatten aufzutreten und zwar sind wenigstens bei *Amphiura squamata* die Ventralplatten den Dorsalplatten immer ein wenig voraus." I have already spoken of this sequence in my account of the side plates. It is here for the first time suggested that the plate *Vv* is the ventral plate of the first or second pair of adambulacrals. If it (*V*) is a ventral plate of the true side plates, it is more rapid in its growth, as compared with the true side plates, than the other and subsequently formed ventrals.

The ventrals *originate on the median ventral line, and are unpaired.* They first appear as a trifid spicule (Fig. 20, *v*), one prong of which is adoral, the others aboral and lateral. In early formation they are free, and do not arise from the lateral arm-plates. They precede, in time of formation, the corresponding dorsal of the same joint; and while in most particulars the growth of the new plates resembles the growth of those of a repaired arm of an Ophiuran as described by Lyman,† the sequence of dorsals and ventrals does not seem to agree with the descriptions by the last-mentioned author, who says that in a repaired arm the upper (dorsal) plate is first formed.

Ventrals never arise by coalescence ot plates on either side of the middle line of the arm.

* *Op. cit.*, p. 189.

† Ophiuridæ and Astrophytidæ, Old and New, *Bull. Mus. Comp. Zoöl.*, p. 258. "Then appear on the central point of juncture, above, clusters of grains which in time grow into upper arm-plates, and a similar process follows for the lower arm-plates." The fact that the dorsal arm-plate in Amphiura originates as a single spicule after the ventral has a meaning as compared with certain embryonic genera.
(See p. 145.)

In a discussion of the relationship of the genus Brisinga to the Ophiurans, A. Agassiz * has sought to show that it is an intermediate genus, connecting starfishes and Ophiurans. He finds the homologues of the ventral plates of the Ophiuran in the fusion of the interambulacral plates along the median line of the arm. He says: "In the case of the Ophiurans . . . the lower arm-plate is formed by the junction of opposing spurs of the interambulacral plates, as can readily be imagined from a comparison with Brisinga, where we find a spur from the interambulacral plates extending nearly two thirds across the arms." That there are anatomical, perhaps embryological, grounds upon which Brisinga may be regarded as reducing the "gap hitherto unfilled between starfishes and Ophiurans," is not doubted; but it may well be questioned whether the ventral plate of Amphiura, originating as it does on the median line and later than the corresponding lateral plates, is homologous to any part of the interambulacral plates of Brisinga.

A. Agassiz † states that "a row of limestone cells extending along the median line separates the base of the suckers," and that the embryo starfish has no trace of any interambulacral system. He calls attention (p. 53) to the absence of a well-defined interambulacral system of plates in a young starfish (Pl. VIII. Fig. 9), in which the rays are well developed, and considers the young starfish as still eminently Ophiuroid in most important embryonic features. He shows a distinct row of "median ambulacral spines (u^1)" on the abactinal side of the arms. These plates with spines are those supposed from A. Agassiz's description to be formed as follows: The radial plates of the abactinal system of the "dorsal part of the arms gradually extend towards the edge of and down on to the actinal side, enclosing the water-system little by little, and finally, as has been described, covering the ambulacral tube," etc. The median plates are later, according to A. Agassiz, ‡ absorbed along the median line in Asteracanthion. It would appear then that from the unabsorbed end of these plates, homologous with the adambulacral plates, grow the ambulacral plates above, or on the abactinal side of the water-system into the position which they eventually have in the adult. In the Ophiurans the median plate of the starfish before absorption of the plate is represented, according to him, by the lower arm-plates (ventrals). The Ophiurans are regarded as remaining in an embryonic condition so far as these plates are concerned.

Aside from the fact already commented upon, that in Amphiura the

* *Mem. Mus. Comp. Zoöl.*, Vol. VI. p. 102.

† Embryology of Starfish, p. 47.

‡ *Op. cit.*, p. 92.

ventral plate is a median actinal deposit, and not, as in the starfish, joined by the growth of plates to the median line to form the embryonic median plate, the author finds this difficulty in the homology indicated above. It would seem from the description that both ambulacral and adambulacral were derived from the same calcification in Asteracanthion, a calcification beginning on the abactinal and growing down on each side to the actinal median coalescence. In Amphiura ambulacral and adambulacral plates are from the first separate and distinct calcifications.

In the abbreviated development of Asterina as given by Ludwig there seems to be a wide difference in the growth of the plates from that of Asteracanthion recorded by A. Agassiz. Adambulacral and ambulacral plates are recorded by the former from the very first, and in the oldest stage figured no embryonic median actinal row of spiniferous plates is figured in the arm. *Asterias glacialis* seems also, according to Lovén's figures, to differ from Asteracanthion in this particular. The plates which appear to correspond with the lateral ambulacra of A. Agassiz's account seem to be separated along the median line of the arm on the actinal side, and median plates below the water-vessel or its position are not figured. Perhaps no genus of starfishes can better serve to explain these discrepancies than Pteraster. The embryology of this starfish is very much needed, and from the interesting fact that the young is carried in a pouch on the abactinal surface of the body, and is therefore probably without a brachiolaria, we may expect interesting revelations from its study.

If one cannot accept the theory that the ventrals of Amphiura are homologous with the embryonic median plates of the young starfish, Asteracanthion, and cannot regard them as formed from the adambulacral plates by coalescence along the median line, it may be asked, What are they, and to what plates in the starfish are they homologous? In answer to this question we might ask another, Why is it necessary to suppose that they are represented in the starfish? We know that there are plates on the dorsal hemisome of Amphiura which seem not to be represented in the starfish. Why not suppose that the ventrals are unrepresented? Perhaps they belong neither to ambulacral nor interambulacral systems, but are special plates for the protection of the nerve and water system of the arms. Perhaps also similar coverings of the Echinoid are also not referable to either ambulacral * or interambulacral systems, as we under-

* Ludwig regards the ambulacral plates of the starfish as unrepresented in the sea-urchin, or highly modified into the auricles. This homology of what are commonly called the ambulacrals in the sea-urchin with the adambulacral of starfishes

stand it, but to special plates not represented in the starfishes, Asteracanthion, or Asterina, young or old.

Dorsal Plates. — The dorsal or upper plates of the arm (Fig. 19, *d*) originate in the median dorsal line as simple trifid spicules, and form in series from the adoral to the terminal, the adoral being the oldest. The last formed is nearest the terminal. In their first condition they resemble the ventrals, and the subsequent growth is similar. The dorsal appears after the corresponding ventral. This fact is an interesting one in comparative anatomy. Many genera of Ophiuridæ (Ophiohelus, Ophiambyx, and others from deep seas) and all the Astrophytidæ are destitute of dorsals. In these Ophiuridæ the ventrals are present, and in the Astrophytidæ the first ventral is developed while others are wanting. The dorsals disappear before the ventrals, if the want of dorsals in these low genera is due to degradation, or the genera have not progressed through embryonic stages in which dorsals appear, if, as is probably the case, dorsals have never appeared. In the growth of Amphiura the ventrals form first, and those genera with a single ventral and no dorsal may be compared with my Fig. 17, Pl. III.

I am led to suppose that the dorsals have been inadvertently omitted in certain of the figures of a young Amphiura by Ludwig (Pl. XI. Figs. 21, 25), for he has not represented these plates in a young specimen in which three pairs of side arm-plates are represented (Pl. XI. Fig. 21, ad^3, ad^4, ad^5). In a young Amphiura of about the same age (Pl. III. Fig. 19) at least one dorsal plate is formed, and in another as old as that represented in his Fig. 25 (same plate) the dorsals have increased in number. In none of Ludwig's figures are dorsals represented, although in Figs. 21, 25, they must have been already formed.

The dorsal originates adaxially to its side plates on the median line, as shown in my figures.

would explain the position of the water-vessel in the former group. We must look with interest to the method of growth of these plates in sea-urchins much younger than any yet studied for a solution of this question.

As the viviparous Amphiura and the Asterina with the direct development have thus far furnished the best information in regard to the method of formation of the plates in Ophiurans and starfishes, perhaps the growth of the plates in Echinoids can best be revealed by the life history of the Hemiaster of the South Sea, with young in pouches in the ambulacral zones. Although the young Hemiaster has been well described by A. Agassiz, Thomson, and others, the growth of the young plates is as yet not well enough known for comparison.

The following summary may be made of the preceding observations:—

1. The intestine of the bisymmetrical larva is early developed, and later in development becomes atrophied and is lost.

2. The mouth and œsophagus (?) of the bilateral larva is formed by an invagination of the epiblast while yet the larva is enclosed in its sac and attached to the parent.

3. The provisional skeleton of the bilateral larva is not always symmetrical, and sometimes develops on one side. The first-formed rod is not always a trifid calcification.

4. An umbilical connection exists in all later stages of growth until the pentagonal form is assumed. The relation of the umbilicus to the mouth, stomach, and intestine is described.

5. The first calcareous plates to form on the abactinal hemisome are five first radials, and a little later a dorsocentral. The radials antedate the terminals.

6. The first plates to form on the actinal hemisome are the first adambulacral.

7. The second pair of adambulacral plates bear club-shaped spines. These last structures are homologous to the spines of the lateral plates of the arms.

8. The first ventral plate to form belongs to the first pair of adambulacral plates, and not to side plates of the arms. This first ventral, although not belonging to the portion of the arm free from the disk, is homologous to the other ventral arm-plates.

9. The radial shields originate before a plate called the "underbasal" forms between the dorsocentral and the primary radials, and while there are but two intermediate plates in each of the interradii.

10. The homology of certain plates of the young Amphiura to the basals, as suggested by Carpenter, is discussed, and doubts advanced whether the individual plates mentioned by him are basals in preference to other interradial plates.

11. The ambulacral plates do not always originate as trifid spicules, but sometimes first appear as parallel unbranched rods.

12. *A. squamata* is infested by a parasitic Crustacean, which, although in adult form closely allied to a Copepod, lays eggs in packets in the host. These ova were found in conditions of cleavage, in a nauplius stage and in intermediate conditions. The adult is also found in the Amphiura. Eggs *not* attached to adult.

The following summary may be made of new figures, or new anatomical details first figured : —

1. Figures (Pl. I. Figs. 1, 2) of plutei of Ophiopholis older than that figured in *Bull. Mus. Comp. Zoöl.*, XI. 4, Fig. 23, and younger than adult. Figure (Pl. I. Fig. 3) of an adult pluteus of Ophiopholis.

2. Figures (Pl. II. Figs. 5, 7, 8) of the umbilical connection of the bilaterally symmetrical young with its parent. These differ from those of Max Schultze in showing the relation of this structure to internal organs. In Apostolides' and Metschnikoff's figures of the bisymmetrical larva this structure is not represented. Figure (Pl. II. Fig. 4) of a larva with a single asymmetrical pluteus spine. Figures (Pl. II. Figs. 13, 14) of the actinal and abactinal hemisome of a young Amphiura of an age between that figured by Ludwig on Pl. XI. Figs. 17, 23, and Pl. XI. Fig. 19.

3. Figure (Pl. III. Fig. 20) of the actinal hemisome of a young Amphiura older than Ludwig's Pl. XI. Fig. 18. This figure shows structures purposely omitted in all Ludwig's figures, viz. spines and club-shaped bodies, appendages of the second pair of adambulacral. Figure (Pl. III. Fig. 17) older than Ludwig's Pl. XI. Fig. 19 and younger than his Pl. XI. Fig. 18, illustrating the formation of the first side plates of the arms. Figure (Pl. III. Fig. 19) illustrating the relative situation of the dorsals. Dorsals are omitted in all Ludwig's figures of the arm from the abactinal side. My figure is younger than his Pl. XI. Fig. 21, in which a dorsal ought to be represented. Figure (Pl. III. Fig. 15) showing the arm-joints or ambulacral plates of the arms *in situ* and before coalescence.

CAMBRIDGE, January, 1887.

EXPLANATION OF THE PLATES.

LETTERING.

a. Opening into the supposed cavity of the blastosphere, blastopore?
ad[1]. First pair of adambulacral plates.
ad[2]. Second pair of adambulacral plates.
al. Anal lobe.
alr. Anterolateral rod.
ar. Anterior rod.
c. Infolded epiblast.
cav. Cavity, segmentation cavity.
cr. Calcareous trifid spicules.
d. Dorsal plate, upper arm-plate.
dc. Dorsocentral plate.
eb. Epiblast.
f. Feeler, leg, paired feeler.
ga. Stomach.
i. Intestine.
ir. Interradial plate.
lp. Lateral arm-plates, adambulacral, side-plates.
lr. Lateral rod.
ls. Lateral "Scheibe," enterocœl on left side.
lw. Left-water tube or hydrocœl.
m. Madreporic opening.
m[1]. Inner layer or envelope of the segmentation spheres.
m[2]. Outer layer or envelope.
mb. Mesoblast.
mbc. Mesoblastic cells } "Mesenchyme?"
o. Oral plate.
os. Ambulacral plates, "ossicles," "arm bones."
oe. Œsophagus.
or. Mouth.
pig. Pigment.
pr. Posterior rod.
ps. Pluteus spine.
rp. Radial plate, first radial.
rp[2]. *rp*[3]. } Plates of disk formed after the first radials.
rs. Radial shield.

rw. Right water-vessel, hydrocœl.
sp. Spine of arm.
spl. Spoon-shaped plate.
t. Teeth.
tf. Unpaired or terminal feeler. See *wt.*
to. Torus angularis, jaw-plate.
tp. Terminal plate, terminal.
u. Connection of pentagonal larva with parent. In stages earlier than pentagonal larva also found.
v. Ventral plate, lower arm-plate.
wt. Terminal end of water-vessel of the arm.

PLATE I.

Figures drawn with Camera lucida, Obj. BB.

Fig. 1. Pluteus of *Ophiopholis aculeata*, Gray, in a little older condition than that figured in Fig. 23, Pl. I., *Bull. Mus. Comp. Zoöl.*, Vol. XII. No. 4.
" 2. The same somewhat older. Seen from side on which mouth opens.
" 3. Adult pluteus of *O. aculeata* before young Ophiuran has begun to form.

The drawings from which these figures were made are from plutei taken at Frye's Island, New Brunswick. This island bears the name of Cailiff's Island on the Admiralty Chart.

The same plutei are common at Eastport, Maine.

PLATE II.

Figures drawn with Camera, Objs. BB, DD, Zeiss. All except Fig. 1 with Obj. BB.

Fig. 1. Blastosphere of *Amphiura squamata.* Diameter, .15 mm.
" 2. Same, younger.
" 3. Gastrula.
" 4. Ventral view of a bisymmetrical larva, unattached.
" 5. The same, lateral view, attached.
" 6. Somewhat older larva than the last, showing the vasoperitoneal sacs or water-tubes.
" 7. The last, lateral view, unattached. The remnant of the attachment in the upper right-hand corner.
" 8. An older larva than the last, attached. Dorsal view.
" 9. The same, older.
" 10. The same, still older.
" 11. Somewhat older larva.
" 12. A pentagonal attached larva with well-formed radial, dorsocentral, and terminal plates. Abactinal view. Attachment at *u.*
" 13. Youngest free Amphiura, unattached to parent. Found free in mother. Abactinal view. The great prominence of two of the terminal plates, *tp*, is due to the position which the specimen had when drawn.

Fig. 14. An older larva from the body of parent. Abactinal view. The club-shaped bodies ad^2 are spines of the second pair of adambulacrals, which in this stage project beyond the periphery of the disk.

PLATE III.

Fig. 15. View of the calcareous plates of the actinal side of the disk of Amphiura in a pentagonal larva younger than Pl. II. Fig. 13.

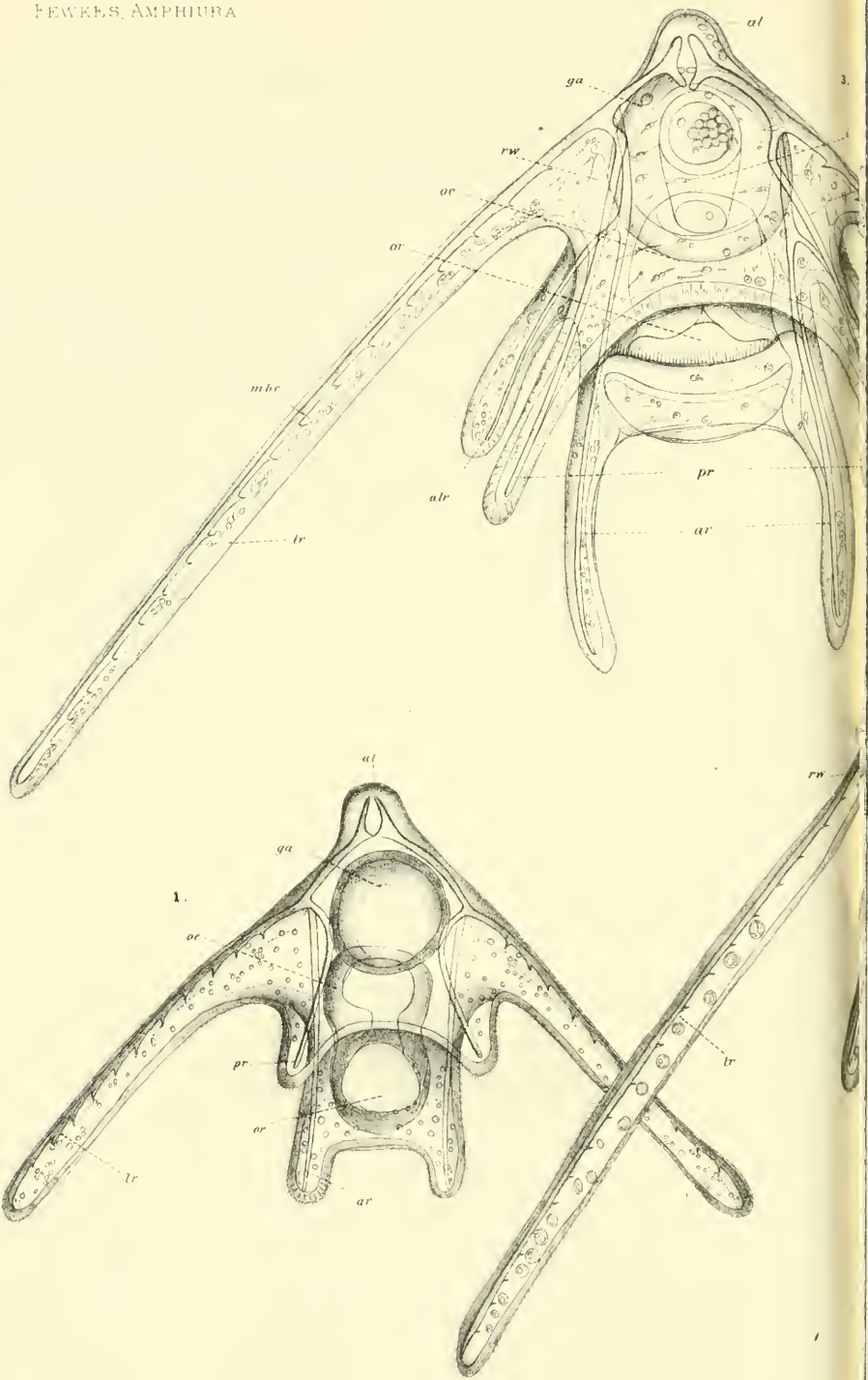
" 16. One fifth of the actinal hemisome of an older pentagonal larva than last. This figure has, in addition to plates of Fig. 15, the ventrals *v*, and orals *o*.

" 17. Pentagonal larva, actinal view, older than last, showing the origin of the lateral plates *lp*.

" 18. Abactinal view of an older larva in which the arms have increased in length, the terminal plate being pushed outward by the formation of the lateral and ventral plates. One arm is shaded, two adjacent arms drawn in outline, and two arms not represented.

" 19. The arm and portion of the abactinal hemisome of an older Amphiura. Three pairs of lateral arm-plates are represented, and two dorsals are shown. Abactinal view.

" 20. An arm and portion of the actinal hemisome of a larva about the same age or slightly older than the last.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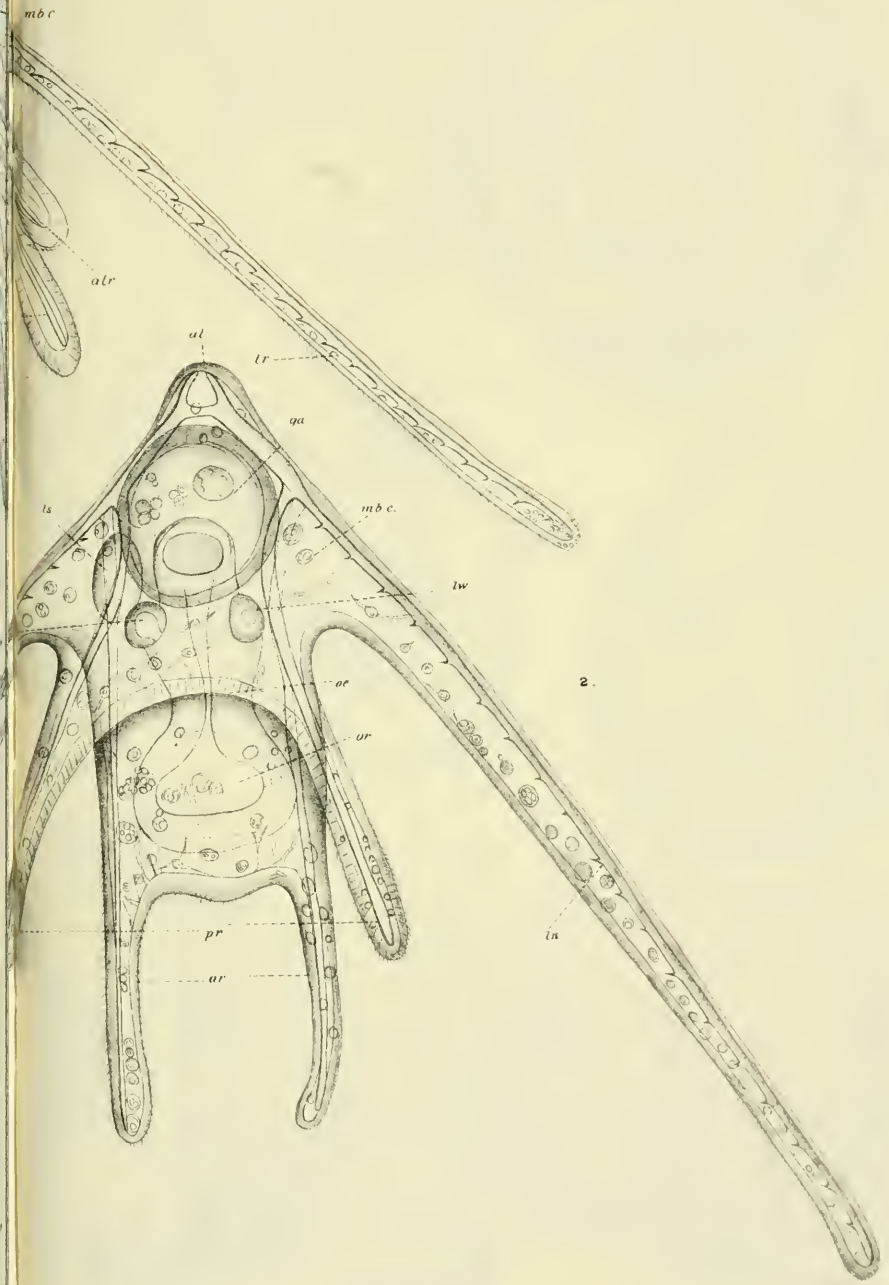
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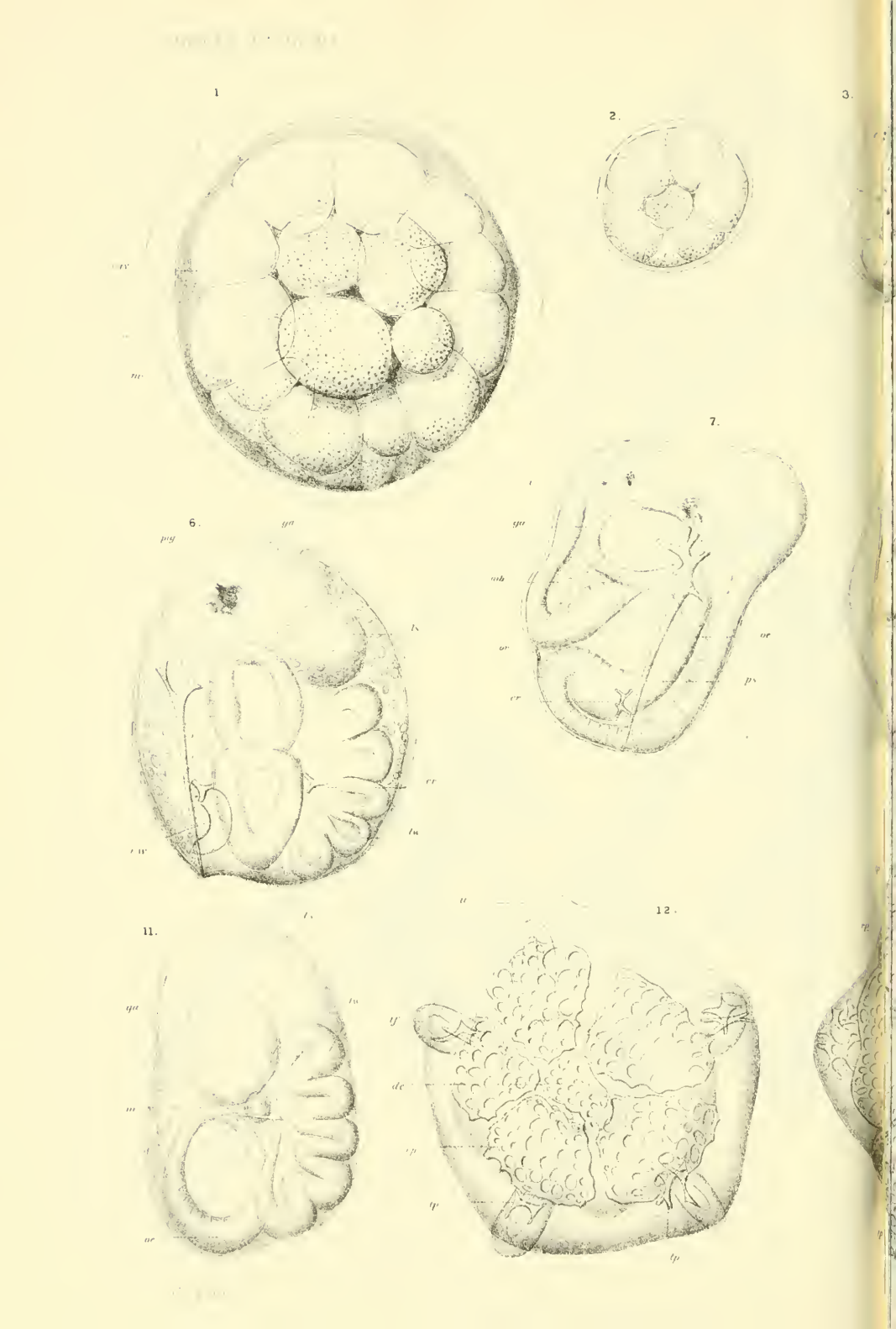
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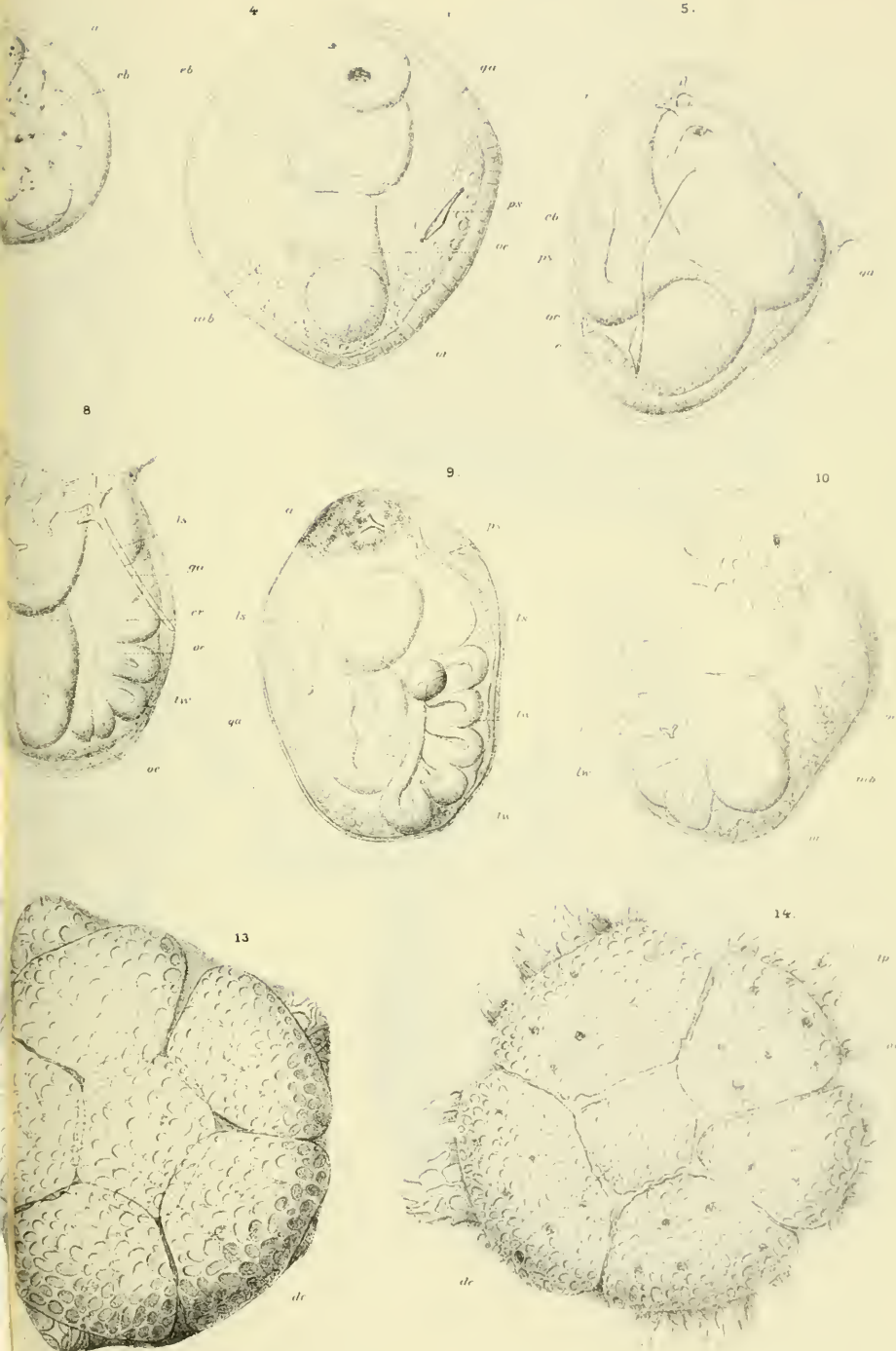
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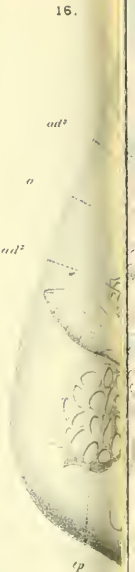

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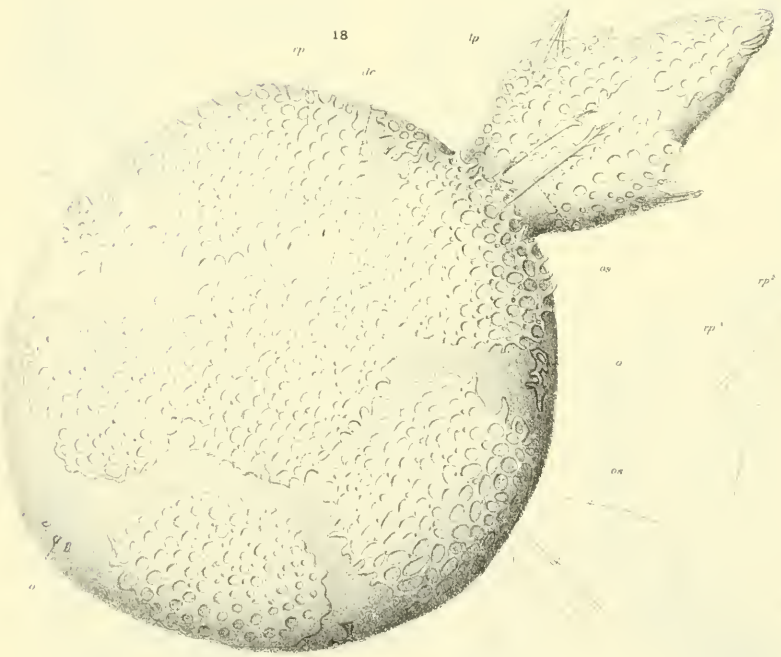

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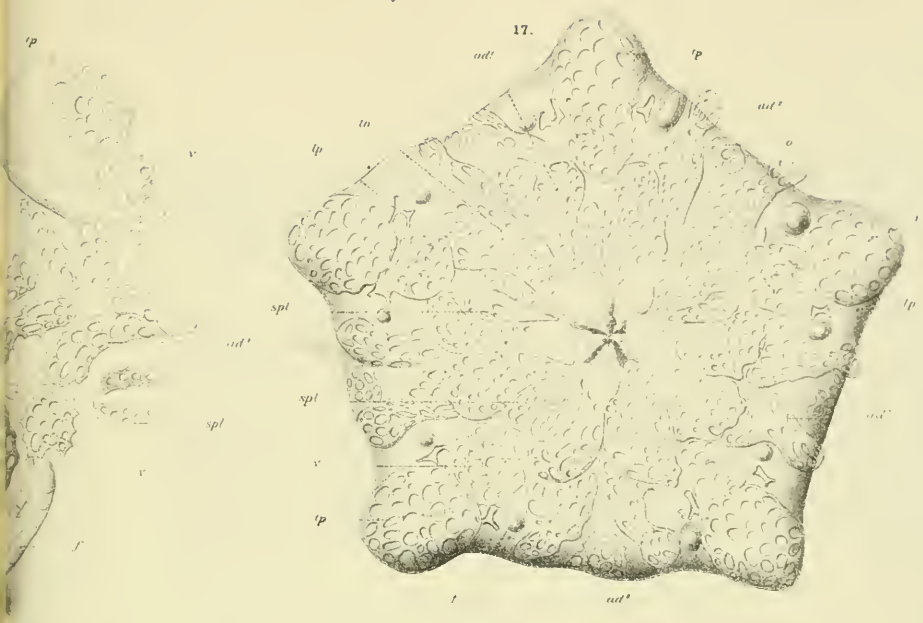

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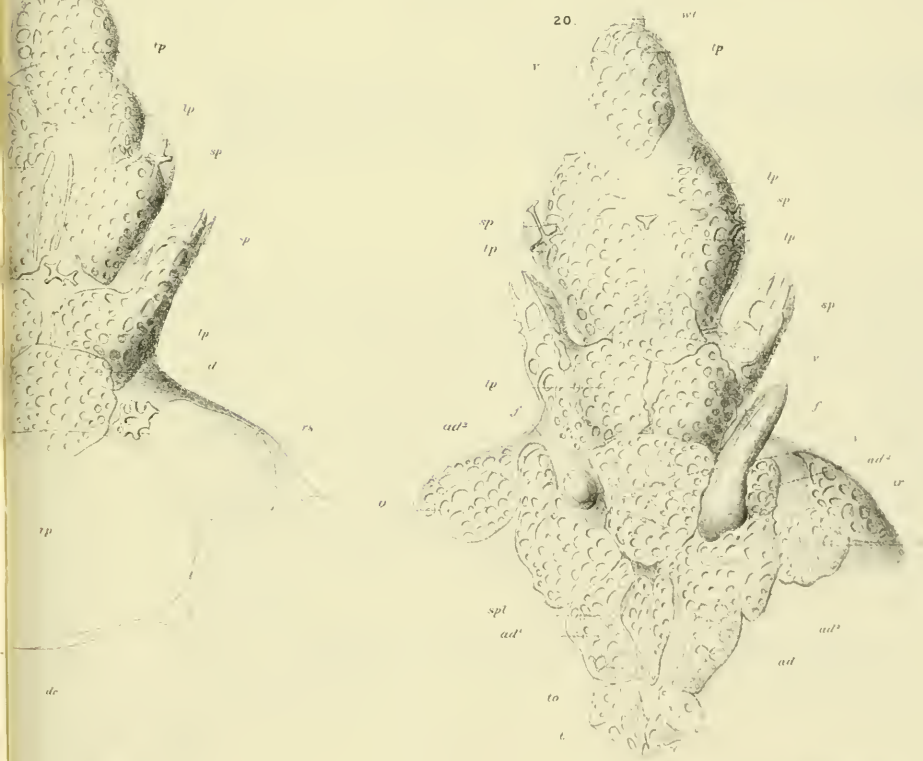


No. 5. — *Preliminary Account of the Fossil Mammals from the White River Formation contained in the Museum of Comparative Zoölogy.* By W. B. Scott and Henry F. Osborn.

This paper is a brief abstract of a memoir upon the Cambridge collection of Miocene Mammals, which is now in preparation. This collection was made by Mr. Samuel Garman in Nebraska and Dakota, and has been very kindly placed in our hands by Professor Agassiz for preparation and description. The work of excavating, cleaning, and mounting the fossils has been for the most part performed by Dr. Franklin C. Hill, Curator of the Geological Museum at Princeton, and to him our best thanks are due. The drawings were all executed by Mr. R. Weber.

Geological Museum, Princeton, N. J., July 9, 1887.

RODENTIA.

Palæolagus Haydeni, Leidy. Several specimens of jaws and teeth represent this species in the collection, but add nothing to our previous knowledge.

Ischyromys typus, Leidy. Isolated teeth.

CREODONTA.

Hyænodon horridus, Leidy. A most valuable and indeed unique specimen of this species, belonging to the Cambridge collection, has already been described by one of us elsewhere.* Here it will suffice to recapitulate some of the more important facts established by it. The posterior dorsal and lumbar vertebræ show the characteristically creodont feature of involuted zygapophyses, such as are not found in any known carnivore. The scaphoid and lunar bones are separate, and a distinct central is found; the manus is plantigrade and pentadactyl, and the ungual phalanges are deeply cleft. This specimen renders it perfectly certain that *Hyænodon* was a typical creodont, and that it was in all probability an aquatic form. It also shows that *Hyænodon* is not at all allied to *Mesonyx*, as has been supposed, but rather to *Pterodon, Protopsalis*, and *Oxyæna*.

* Scott, Journ. Acad. Nat. Sci. Phil., Ser. 2, Vol. IX. No. 2.

Hyænodon leptocephalus, Scott.* This species is peculiar for the long, narrow cranium, and for the position of the posterior nares, which are roofed in by the entire length of the palatines and by the pterygoid plates of the alisphenoid. In size it slightly exceeds the *H. crucians* of Leidy. This species was established upon two fine skulls in the Cambridge collection.

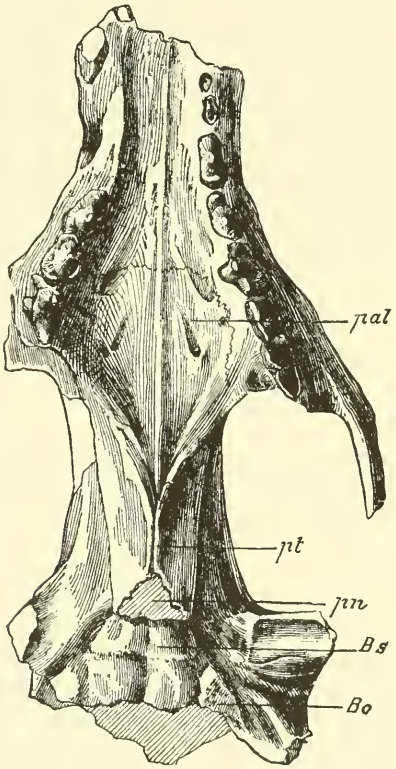


FIGURE 1. – Skull of *Hyænodon leptocephalus*, from below upon the under surface.

CARNIVORA.

CANIDÆ.

Cynodictis (Amphicyon) gracilis, Leidy. With the possible exception of some specimens from the Uinta eocene, the genus *Amphicyon* has not been found in America. *Galecynus*, as has been lately shown,† cannot be separated

* *Loc. cit.*

† Huxley, P. Z. S., 1880, p. 280 ; Lydekker, Brit. Mus. Cat. Foss. Mam., Vol. I.

from *Canis*. The American species which have been referred to *Amphicyon* and *Galecynus* in reality belong to *Cynodictis*, which has the same dental formula as *Canis*, but differs in the construction of the teeth.

CRYPTOPROCTIDÆ.

Dinictis felina, Leidy. This genus has usually been placed in the same family with *Hoplophoneus;* but the materials now at command show that it is quite distinct, and more nearly allied to the recent Madagascar form *Cryptoprocta*. There are several cranial and skeletal fragments in this collection which are of much interest. The radius has the same shape as in *Hoplophoneus*, with a concave disk-shaped head and expanded distal end. The tibia has a very much flattened astragalar facet, and the astragalus has not such a deeply grooved trochlea as in *Hoplophoneus;* the phalanges of the second row have an excavation on the outer side, showing that the claws were retractile. A very fine specimen in the Princeton Museum, of which an account will shortly be published, brings out the resemblance to *Cryptoprocta* very clearly; as in that animal, the foot is pentadactyl and completely plantigrade, and the ungual phalanges were simple, compressed, and without bony hoods.

NIMRAVIDÆ.*

Hoplophoneus (Drepanodon) primævus, Leidy. Numbers of fine specimens of this species are preserved in the collection, which with some of the Princeton material enable us to give a restoration of this very interesting type. The vertebræ are for the most part like those of the true cats, but with some resemblances to *Cryptoprocta*. The scapula has a prominent spine, with acromion and metacromion. The humerus is remarkable for the great prominence of the deltoid ridge; there is a very prominent internal condyle and large epicondylar foramen; the trochlea is like that of the true cats. The ulna and radius are essentially feline, and need no especial description. The carpus is also feline, but has a small vertical diameter; the scaphoid and lunar have coalesced (the first case reported from the White River formation), though the line of junction is still clearly visible. The metacarpals are five in number, the pollex very much reduced, and the other digits small and slender. The ungual phalanges show an unexpected degree of specialization; they are compressed, curved, and have a large lamina of bone reflected over their base as in the higher *Felidæ*, and a strong process for the tendon appears below the articular facet. These phalanges are very different from those of *Cryptoprocta*, *Dinictis*, and *Procælurus*. The pelvis is in general like that of the *Cryptoproc-*

* If Cope's definition of this family (Tert. Vert., p. 948) be accepted, *Hoplophoneus* cannot be included in it. We do not consider, however, that the absence of the hallux is a good family character, while the foot structure of *Hoplophoneus* shows that it should be placed in a separate family from *Dinictis*, for which the name *Nimravidæ* may be retained.

tidæ. The femur is rather long and slender, and has a distinct third trochanter, which is also to be seen in *Cryptoprocta*, *Dinictis*, *Procælurus*, and *Amphicyon*, and is probably an inheritance from their creodont ancestry. In appearance the femur of *Hoplophoneus* closely resembles that of *Procælurus* as figured by Filhol.* The tibia is stout, laterally compressed, and curved forward; the distal end is broad, and not very deeply grooved, and with heavy malleolus. The fibula has a slender shaft and expanded distal end. The tarsus is feline, but with some differences; the astragalus is more flattened than in the true cats, and the calcaneum has the arctoid character of a conical process on the outer side near the distal end (found also in *Amphicyon*, *Procælurus*, and *Dinictis*). The metatarsals, five in number, are slender and weak; the three external ones are strongly interlocked, as in the cats.

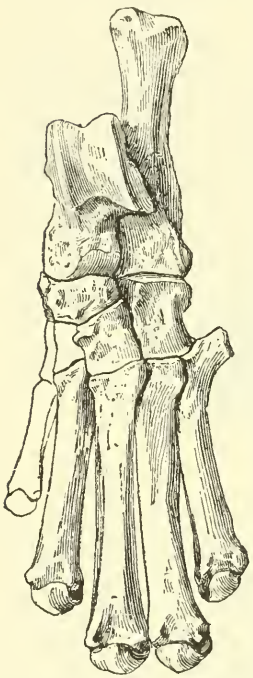


FIGURE 2. — Left hind foot of *Hoplophoneus*, viewed from in front.

Restoration (see Plate I.). — This animal had a very striking appearance, with its short rounded head and exceedingly long and trenchant canine tusks; the neck is long, the trunk, especially the lumbar region, is short as compared with *Cryptoprocta;* the tail is very long, as in nearly all of the early flesh-eaters; the limbs were stout, the feet on the contrary very weak, as in the creodonts. The structure of the foot renders it all but certain that this animal was digitigrade, though some features of its plantigrade ancestry, as the articulation of the astragalus with the cuboid, are retained. *H. primævus* was a small animal, standing hardly more than 18 inches high and about 33 inches long, exclusive of the tail.

Hoplophoneus occidentalis, Leidy. This is a larger species, equalling the puma in size, and with a more robust skeleton.

ARTIODACTYLA.

OREODONTIDÆ.

Oreodon Culbertsoni, Leidy. This very common and well-known species is represented by numerous skulls and parts of the skeleton.

Oreodon gracilis, Leidy. Little has hitherto been known as to the

* Soc. Sc. Ph. et Nat. Tours, 1880, Pl. V. fig. 3.

skeleton of this species ; it is relatively lighter and more slender than in the larger species, but otherwise not different from it. Most important is a specimen containing all the metacarpals and phalanges in undisturbed position, and this shows most distinctly the presence of the pollex, as one of us* had previously shown to be true in the case of *O. Culbertsoni*. This correspondence between the two species removes all suspicion that the pollex in the specimen first described might be a case of abnormal polydactylism. The discovery of a five-toed artiodactyl is of the utmost importance, as it furnishes the demonstration of what has long been surmised, that the ungulates of both odd and even-toed series have been derived from pentadactyl forms.

Eucrotaphus (Oreodon) major, Leidy (*Eporeodon major*, Marsh). This genus differs from *Oreodon* in the presence of large inflated tympanic bullæ, and also (*fide* Marsh †) in the absence of a pollex. The dentition and character of the skull are identical in the two genera.

Agriochœrus latifrons, Leidy. Isolated jaws and teeth.

SUIDÆ.

Hyotherium (?) americanum, sp. nov. There is in the Princeton Museum a suilline skull from the White River formation, which cannot be correlated with any of Dr. Leidy's genera. It agrees very closely and is probably identical with the *Hyotherium* of Europe, and will be provisionally referred to that genus. In the Cambridge collection there is a suilline hind foot, which may be referred to the same species. The astragalus is very oblique, the external condyle greatly exceeding the internal in size ; the neck is short and the distal end broad ; the calcaneal facets are confluent. The cuboid is low, broad, and deep (antero-posteriorly). The metatarsals are very suilline in character, the median pair short and massive, the laterals shorter and especially more slender ; the proximal ends are all on the same transverse line, and the articular faces nearly plane ; the trochlear ridges on the distal ends are confined to the posterior aspect, thus differing from *Sus*, *Dicotyles*, and other recent genera. The phalanges of the median digits are heavier but not much longer than those of the lateral digits.

Measurements.

	M.
Astragalus, length (outer side)	.032
" width trochlea	.019
Cuboid, length	.016
" width	.015
Metatarsal II., length	.048
" III. "	.063

* Scott, Proc. Am. Ass. Adv. Sci., 1884, p. 493.

† Dinocerata, p. 187, fig. 162.

Metatarsal IV., length	.068
" V. "	.055
Proximal phalanx, digit IV., length	.025
" " " IV., width proximal end	.013
" " " V., length	.022
" " " V., width proximal end	.011

Entelodon (Elotherium) Mortoni, Leidy. Represented by several skulls in good preservation, one of which is particularly interesting as showing the milk dentition. This will be fully described in our final paper.

HYOPOTAMIDÆ.

Hyopotamus americanus, Leidy. Represented by fragments of lower jaws with molar teeth.

CAMELIDÆ.

Pœbrotherium Wilsoni, Leidy. Two skulls, one of which exhibits the milk dentition, represents this species.

TRAGULIDÆ.

Leptomeryx Evansi, Leidy. Rütimeyer* has recently questioned the propriety of referring this genus to the chevrotains, and considers it more allied to the *Camelidæ*. In consequence of this opinion from such a distinguished source, we have carefully examined the dentition and skeleton of the genus, and are now in position to give a nearly complete account of it, which will be done in the final paper. Here we need only record the conclusion reached, that *Leptomeryx*, though exhibiting several points of divergence from the modern genera of the family, is nevertheless a true traguline. We thus reach a different conclusion from Rütimeyer on this subject, and agree with Schlosser.†

GENUS INCERTÆ SEDIS.

Hypisodus minimus, Cope. This minute ruminant is the earliest known hypsodont form found in America. Professor Cope gives the dental formula as I. $\frac{?}{3}$, C. $\frac{?}{1}$, Pm. $\frac{?}{4}$, M. $\frac{3}{3}$; and states that "in the mandibular series the six incisors, two canines, and two first premolars form an uninterrupted series of ten subequal teeth, and are followed by a long diastema."‡ The genus has hitherto been known only from the dentition, but there is fortunately in this

* Abh. d. schweiz. pal. Gesell., Bd. X. p. 98.
† Morph. Jahrb., Bd. XII. p. 75.
‡ U. S. Geol. and Geogr. Surv. Terr., 1873, p. 501.

collection the well-preserved facial part of a skull, together with the lower jaws; hardly enough, however, to make the systematic position of the animal entirely clear. The orbits are very large and deep-set, as in the tragulines, and separated by a mere septum; the lachrymals have a considerable extent vertically, but extend little on the side of the face, and do not reach the nasals; the maxillaries are proportionately higher than in *Leptomeryx;* the nasals are much contracted; the palate is well arched from side to side, and the palatines seem to be shaped much as in *Tragulus;* the mandible is very slender.

The last upper premolar is composed of an external and internal crescent, enclosing a valley between them; the third and second are very small and apparently secant, without internal cusps; the first, if present at all, was evidently separated from the second by a considerable diastema.

PERISSODACTYLA.

MENODONTIDÆ.

MENODUS, Pomel.

Syn. *Titanotherium*, Leidy. *Megacerops*, Leidy. *Brontotherium*, Marsh. (?*Symborodon*, Cope.) *Diconodon*, Marsh.

Generic Characters. — Dentition: I. $\frac{2}{2}$ (variable), C. $\frac{1}{1}$, Pm. $\frac{4}{3}$, M. $\frac{3}{3}$. The incisors are small and variable in number. The upper and lower median incisors are usually wanting. Molars and premolars alike, resembling those of *Chalicotherium* in pattern. A stout pair of transversely placed horns developed from the frontals and nasals.

There are three skulls in this collection and the horns of several others, representing four or five species which may readily be distinguished. The chief difficulty is in deciding where to draw the generic lines, which is increased by the fact that the mandibles are seldom found associated with the skulls. As in *Uintatherium*, the variability in the various portions of the skull, especially in the region of the horns, is so extreme, that no two skulls are found which are exactly alike. But the dentition, which is constant among the *Dinocerata*, here greatly complicates the problems of classification. The premolars vary in number, and the incisors, always of relatively small size, and fairly constant in number in the upper jaw, vary from three to none in the lower jaw.* In all the lower jaws found in Professor Cope's collection of *Menodontidæ* from Northern Colorado there are no incisors, and the mandibular symphysis is extremely narrow. In the lower jaws of the Cambridge and Princeton collections, which are all from the Nebraska and Dakota exposures, the symphysis is broad, and the incisors where preserved are two in number, while in one of the Cambridge specimens no less than three incisor alveoli may be counted upon one side of the symphysis.

* One of the Cambridge skulls has but a single upper incisor, *M. coloradensis.*

We might infer from this that *Symborodon* can be clearly separated from *Menodus* by the absence of the lower incisors, accompanied by a narrowing of the symphysis; but Professor Cope has recently described a new species, *M. angustigenis*, from the Swift Current Creek region,* which combines the narrow type of symphysis with the presence of two incisors. The separation of these genera is rendered still more improbable by the parallelism which exists between the skulls from the Nebraska and Colorado localities, especially in respect to the conformation of the nasal bones and the horns. The genus *Symborodon* is however provisionally adopted at present to include the species with a narrow mandibular symphysis and no lower incisors.

The genus *Brontotherium*, Marsh, cannot be distinguished from *Menodus*. It rests in part upon the premolar formula, $\frac{4—4}{3—3}$, in the synopsis given by Professor Marsh,† as distinguished from *Menodus* with ? Pm. $\frac{4—4}{4—4}$. One of the lower jaws of the Princeton collection, however, has the premolar formula $\frac{3—4}{}$, demonstrating that the first lower premolar is a variable tooth, and cannot in this case be used in classification. The same rule applies to the second cone upon the last upper molar, the supposed generic character of *Diconodon*, Marsh. This is found in different species in all degrees of development, from a small prominence upon the basal cingulum to a well-developed cone (*M. Proutii*).

Such characters as the invariable absence of lower incisors may subsequently be found to separate one genus of the *Menodontidæ* from another; but our present evidence goes to show that they simply characterize the extremes of a closely related series of animals, from the same horizon, of which the intermediate forms are represented by numerous species. The safest basis of specific determination seems to be the correlation between the development and proportion of the horns and of the nasals, the rule being that where the horns are long the nasals are short, and conversely. The number of the teeth does not at present seem to be absolutely constant, even within the limits of the species.

The following determination of the species in the Cambridge collection is, for the above and other obvious reasons, provisional. The classification can be finally settled only when the lower jaws and skulls are found in association. If, for example, a large number of forms of the *M. coloradensis* type of skull are found with but a single upper incisor, they will undoubtedly represent a species distinct from both *S. trigonoceras*, Cope, and *M. ingens*, Marsh.

M. coloradensis, Leidy, 1870. Syn. *M. ingens*, Marsh, Am. Journ. Sci. and Arts, 1874. *S. trigonoceras*, Cope, Synopsis New Vert. Col., 1873, p. 13.

The type of this species, a snout with horns and nasals, was figured by Pro-

* The Vertebrata of the Swift Current Creek Region of the Cypress Hills. Geol. and Nat. Hist. Surv. of Canada, 1886, p. 81 c.

† Am. Journ. Sci. and Arts, 3d Ser., XI. 339.

fessor Leidy * in 1873, and agrees closely with the corresponding portions of the smallest skull in the Cambridge collection, both in form and measurement. The skull is entire, and enables us to fully define this species.

Dentition: I. $\frac{1 \text{ or } 2}{1}$, C. $\frac{1}{1}$, Pm. $\frac{4}{4}$, M. $\frac{3}{3}$. No diastema behind the canine. Second upper incisor sometimes wanting. First upper premolar small. Last upper molar without distinct second cone. Upper premolars with a strong internal cingulum. Anterior nares transversely broad and shallow vertically. Nasals long and broad. Horns short and stout, obliquely compressed at the base so that their faces point in three directions, erect and slightly recurved when viewed from the side. The greatest diameter at the base is fore and aft. Orbits large, and widely open. Superciliary ridge not prominent. Zygomatic arches broad and powerful, but without flanges. Post-glenoid and post-tympanic processes separate or not broadly united.

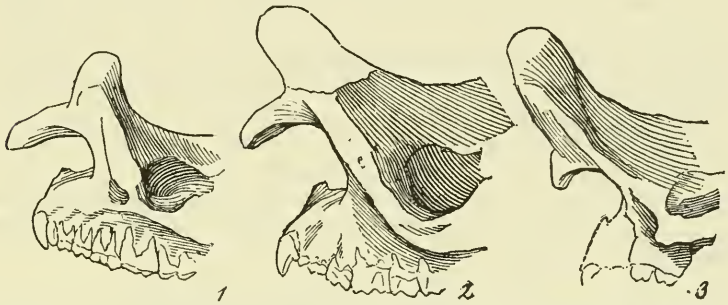


FIGURE 3. — Anterior portion of the skull of three species of *Menodus*, showing the relations of the nasals to the horns in side view. 1. *M. coloradensis*. 2. *M. tichoceras*. 3. *M. dolichoceras*.

The skull of this individual is considerably smaller than the type of *M. ingens*, measuring only 27½ inches from the occipital condyles to the tips of the nasals. The superciliary ridges expand into small postorbital processes, which are wanting in the above type. The post-glenoid processes do not touch the post-tympanic. The *M. ingens* skull has two incisors, while this specimen has but one. It is possible that one or more of the above differences may prove to be of permanent specific value, but in the conformation of the nasals and of the horns, as well as in all other details of proportion, these skulls are apparently closely similar.

In comparison with the type of *S. trigonoceras*, Cope, the horns and nasals have somewhat similar proportions, but are less distinctly triquetrous at the base. The skull also resembles that of *M. angustigenis*, Cope.

M. tichoceras, sp. nov. This species may prove identical with *S. altirostris*, Cope. Dentition: I. $\frac{2}{2}$, C. $\frac{1}{1}$, Pm. $\frac{4}{4}$, M. $\frac{3}{3}$.† No diastema behind the canine.

* Extinct Vertebrate Fauna, etc., U. S. Geol. Surv., Vol. I. Plate I.

† The number of lower incisors is inferred from the distinctly worn tips of the upper incisors.

Second cone on last upper molar united with the cingulum. Probably two lower incisors. Upper premolars with a faint or no internal cingulum. Nasal bones intermediate in length and narrowing anteriorly. Horns elongate, subcylindrical in section at the base, and in side view inclined obliquely forward, so as to partly overhang the snout. Anterior nares transversely narrow and vertically deep, so that the snout is very elevated. Superciliary ridge prominent, rugose, and overhanging the temporal fossæ. Orbits rather small and enclosed. A post-orbital process. Zygomatic arches wide and partly flanged. Post-glenoid and post-tympanic processes widely united.

Description of Skull. — The type of this species is a single large skull, with the dentition complete, and lacking the upper part of the horns and the crest of the occiput. The total length is 29 inches, while Professor Cope's type of *S. altirostris* measures but 25½ inches. The separation from the latter species depends upon the number of lower incisors. Apart from size, the chief distinction from *M. Coloradensis* is in the narrow and elevated terminal portion of the skull, giving a widely different appearance in front view. The zygomatic arch is very massive, and presents a bulge in the posterior half, which however is much less prominent than in *S. bucco*, Cope.

It is also distinct from *M. Proutii*, Leidy. In the Princeton collection is a large skull which has been referred to this species. It differs from *M. tichoceras* in the presence of a diastema behind the superior canine, as well as in the presence of a distinct second cone upon the last upper molar, and of a strong internal cingulum upon the premolars.

M. dolichoceras, sp. nov. This species may prove identical with *S. acer*, Cope. Dentition: I. ?, C. $\frac{1}{1}$, Pm. $\frac{4}{4}$, M $\frac{2}{2}$. Upper premolars with a faint internal cingulum. Nasal bones extremely short and obtuse. Horns extremely long and powerful, directed obliquely forwards and outwards, projecting beyond the nasals in side view. The section is sub-oval at the base, with the long axis obliquely transverse. Cranium very broad and saddle-shaped above the orbits, narrowing somewhat posteriorly. A prominent and overhanging superciliary ridge. Post-glenoid and post-tympanic processes united for a short distance. The skull which we have made the type of this species is much larger and more powerful than Professor Cope's type of *S. acer*. The horns are longer and more widely divergent at the base. The angle of inclination of the horns and the diminutive proportions of the nasals, as well as the form of the top of the cranium, all bring this specimen near *S. acer*, and separate it from other known species. Unlike *S. acer*, the horns are not united by a ridge. The specimen is incomplete in the supra-occipital region, the zygomatic arch is fragmentary, and the maxillary, palatine and basi-occipital regions are much distorted.

M. platyceras, sp. nov. The type of this species is a pair of horns with the nasal bones attached. All other portions of the skull are wanting.

The dentition is unknown. Nasal bones extremely short and obtuse, as in

M. dolichoceras and *M. acer*. The inner contour of the horns is concave; they are greatly flattened antero-posteriorly with a ridge-like outer margin, and connected by a well-raised median ridge. The posterior face is nearly plane,

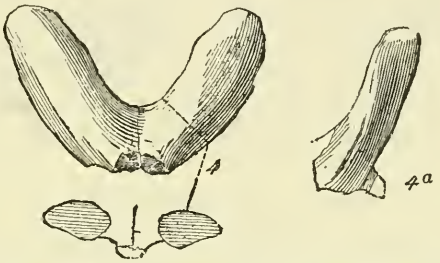


FIGURE 4. — Horns of *M. platyceras*. 4. Viewed from in front and in section. 4a. Viewed from the side.

the anterior is convex, so that the section of the horn is plano-convex from base to tip. In side view the horns completely overhang the nasals, and are slightly recurved. The long axis of the horn section is directly transverse.

MEASUREMENTS.

	Occipital condyles to nasal tips.	Nasal tips to ridge between horns.	Distance between tips of horns, outside measurement.	Length of horns measured from tips to median fronto-nasal suture.	Antero-posterior diameter of the molar-premolar series.	Free portion of nasals.		Approximate diameter of anterior nares.	
						Length.	Breadth.	Vertical.	Transverse.
	M.	M.	M.	M.	M.	M.	M.	M.	M.
M. coloradensis	.70	.16	.33	.16	.31	.08	.12	.075	.135
M. tichoceras	.80?	.13	....	....	.34	.06	.13	.11	.09
M. dolichoceras	.74	.09	.58	.32	....	.04	.09	.075	.075
M. platyceras	....	....	.42	.25	....	....	....	....	....
M. Proutii	.91?	....	....	.20	.37	....	....	....	....

The above measurements bring out very clearly the decrease in the proportions of the nasals *pari passu* with the gradual elongation of the horns. Another very interesting fact is brought out by the comparison of the transverse and longitudinal diameters of the horns at the base. As we pass from the short to the long horned types, through *M. coloradensis*, *tichoceras*, *dolichoceras*, and *platyceras*, there is a gradual rotation of the longer axis of the horn-section from a fore and aft to a transverse plane; the species last named representing the extreme of the transverse type.

FIGURE 5. — Skulls of three species of *Menodus* in front view, showing the variations in the horns, nasals, and anterior nares.

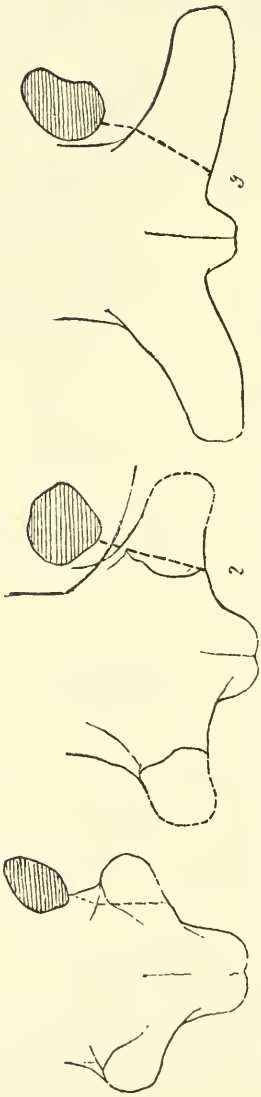


FIGURE 6. — The same skulls viewed from above, showing the nasals and horns, and sections of the bases of the horns.
1. *M. coloradensis*. 2. *M. tichoceras*. 3. *M. dolichoceras*.

The accompanying figures show the four types of skull as seen in the fronto-nasal region. The first type, with long nasals and short erect horns, is represented by *M. coloradensis* and characterizes also *M. ingens* and *M. angustigenis*. The second type, with medium nasals and short obliquely placed horns, is

represented by *M. tichoceras*, and characterizes *M. Proutii* and *M. altirostris*. The third, with short obtuse nasals and long horns, is represented by *M. dolichoceras*, *M. acer*, and *M. platyceras*.

There are doubtless other species of *Menodus* in this collection, but the foregoing are the only fully defined types. The lower jaw with three lower incisors probably belongs to a new species. There is also a pair of diminutive horns, resembling those of *S. heloceras*, Cope. Another pair of horns presents a small knob upon the antero-interior surface, about half-way to the tip, which gives the horn quite a different aspect from those above described.

Restoration of M. Proutii.

The accompanying restoration of *Menodus* (see Plate II.) is from materials in this collection, in the E. M. Museum of Princeton, and in the collections of Professor Cope, as follows: Mus. Comp. Zoöl., the fore and hind limbs and fore feet. E. M. Museum, the pelvis, hind feet, anterior dorsal vertebræ, the cervical vertebræ, the anterior ribs, and skull. The scapula and outlines of the processes of the cervical vertebræ and spines of the first and second dorsal vertebræ are from the Cope collection. The outlines of the phalanges of the fore foot are from specimens in the Cambridge collection, and from Professor Marsh's drawings. All the structures which are wholly or in part conjectural, such as the sternum, the outline of the scapula, the lumbar vertebræ, and sacrum, are drawn in plain or dotted lines without shading. On the other hand, several of the ribs which are known from the Princeton collection are not shaded, for the sake of uniformity. Several of the posterior dorsal vertebral centra are shaded for the relief effect. The proportions of the neck, back, and pelvis, with those of the skull, are known from the fact that these parts in the Princeton collection belong together, i. e. to one individual. The larger bones of the fore and hind limbs are also, for the most part from a single individual; and a number of vertebræ found with the head of a radius of another individual enable us to determine the proportion between the fore limb and the centra of the dorsal vertebræ. The size of the scapula, which belonged to an isolated series, was fixed by the proportions which obtain between this bone and the humerus in the *Proboscidia*, *Rhinocerida*, and *Dinocerata;* viz. that the scapula varies from $\frac{4}{5}$ to $\frac{5}{4}$ the length of the humerus. We have given it $\frac{4}{4}$ the humerus length.

The animal is placed in an erect standing position, the right leg being drawn slightly back. The fore limb is placed nearly at the maximum of extension; the angle of this limb, as indicated by the articular facets of the head and trochlea of the humerus, being intermediate between that of the elephant and rhinoceros. It was capable of being flexed to a much greater degree than is here represented, so as to bring the animal nearer the ground.

The skull and neck, to which the trunk and limbs are proportional, probably belong to *M. Proutii*, a species of about the medium size attained by these animals; for, judging by the measurements of the skulls which are known,

there were other species both smaller and larger. This animal was about eight feet high at the shoulder, and over twelve feet long. The height is greatly increased by the extraordinary development of the spines of the anterior dorsal vertebræ. These are well preserved, and in two cases complete to the tip, in the materials at our disposal. They are broad and flattened nearly to the tip, so as to fit closely together. The neck is longer than that of *Uintatherium*, but shorter than that of the rhinoceros. With the power of flexing the elbow, the head could readily be lowered to the ground in feeding. The arm, fore-arm, and shoulder-blade are decidedly rhinocerotic in character, although showing a greater proportional length and less flexion capacity. The thigh and lower leg, on the other hand, are rather elephantine in their shape and proportions, and indicate much less play at the knee-joint than in the rhinoceros. The limb bones are relatively shorter than in *Uintatherium*, but the metacarpals and tarsals are much longer and less spreading, thus adding considerably to the height. These segments, combined with the elongation of the dorsal spines, gave *Menodus* as great a height as was attained by the eocene genus, with its longer limbs.

AMYNODONTIDÆ.

Rhinoceros-like animals, as far as yet known, extending from the Middle and Upper Eocene (Bridger Beds) to the White River Miocene Beds ; hornless ; canines and incisors present in the typical number in both jaws ; pattern of the premolar transitional to that of the molars; first upper premolars rudimentary or wanting; pattern of true molars like that of the rhinoceros, but with the transverse crests simple; skull with a powerful sagittal crest.

AMYNODON,* Marsh.

Probable syn. *Orthocynodon*, Scott and Osborn.†

Dentition: I. $\frac{3}{3}$, C. $\frac{1}{1}$, Pm. $\frac{4}{4}$, M. $\frac{3}{3}$. Upper canines obliquely placed; lower canines erect and placed immediately in front of the upper when jaw is closed. The third and fourth upper premolars only approach the molar pattern by the development of double transverse crests. First upper premolar small and single fanged. Post-glenoid and post-tympanic processes separate.

* This Eocene genus, owing to the imperfect condition of the type skull in Professor Marsh's collection at the time of description, was incorrectly defined, (Am. Journ. Sci. and Arts, 3d Ser., Vol. XIV. p. 251,) and the present writers, after a personal examination, were led to believe that the type specimen of *O. antiquus* represented a distinct genus. It now proves to be the same, as far as we know at present.

† E. M. Museum Bulletin, No. 3, May, 1883.

METAMYNODON, gen. nov.

Dentition : I. $\frac{3}{3}$, C. $\frac{1}{1}$, Pm. $\frac{3}{2}$, M. $\frac{3}{3}$. Upper and lower canines obliquely placed, the latter fitting somewhat internal to the former when the jaw is closed. The first upper premolar wanting; the second, third, and fourth premolars are of the molar pattern. Post-glenoid and post-tympanic processes widely united.

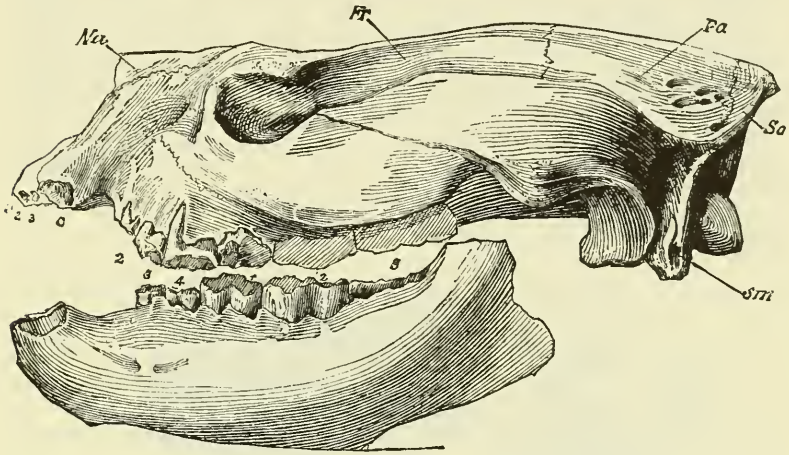


FIGURE 7. — Skull of *Metamynodon planifrons*, in side view, about one sixth natural size.

Metamynodon planifrons, sp. nov *Specific characters.* First upper molar with an incomplete internal cingulum. Lower median incisors small. The molars greatly exceeding the premolars in size.

This genus is represented by a single skull in fine preservation, and the anterior portion of the left mandibular ramus. The latter specimen was found some little distance from the skull, but for many reasons may be safely placed with it. The canine-incisor formula is the same, and the diameters of the canine fangs are similar. There is one less premolar, but the molar-premolar series as a whole has the same antero-posterior length.

Metamynodon is evidently a highly modified successor of *Amynodon*, of about double its size and strength. The dentition is reduced by the loss of one upper and two lower premolars. The pattern of the premolars presents a slight progression in the complication of the transverse crests of pm^2; but as a series they show a decided retardation of growth as compared with the molars which assume very large proportions. The mandibular symphysis is relatively much narrower. The sagittal crest is still more powerful. The skull is modified by the unusual shortening of the facial region, and the flattening of the cranium and broadening of the zygomatic arches, but without the develop-

ment of horns or other protective structures. It equalled in size the largest of the modern rhinoceroses, and belongs to a line which is quite distinct from that of either *Hyracodon*, *Aceratherium*, or *Diceratherium*. The great reduction of the premolar series separates it from the first, while the retention of the full canine-incisor series separates it from the last two lines of descent.

The *skull* is remarkably broad and flat, with powerful and widely extended zygomatic arches, and a long flattened cranium, surmounted by a strong sagittal crest. The antorbital or facial region is considerably less than one third the entire length of the skull, instead of one half the length, as in *Amynodon* and the modern rhinoceroses. The occiput is low, and projects considerably behind the condyle. The small proportions of the facial region and great development of the area of attachment for the muscles of the lower jaw are respectively in direct relation to the unusual reduction of the premolar series and the great size of the molar and canine-incisor series. With these numerous peculiarities, the skull still retains a rhinocerotic character and has unmistakable resemblances to that of *Amynodon*.

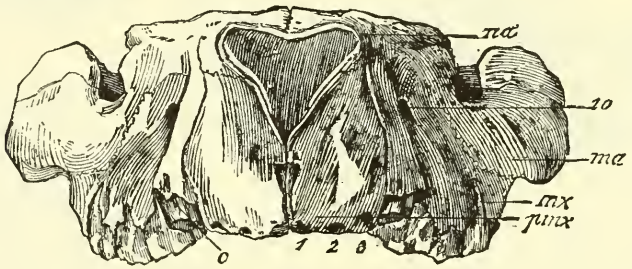


FIGURE 8. — Skull of *Metamynodon*. Front view.

The *premaxillaries* are broad and flattened above, and, bulging forwards, converge into the broad rounded alveolar border. They are quite distinct in the median line. The *anterior nares*, as viewed from in front, are triangular, bounded above by the short, flattened obtuse *nasals* which overlap the inner faces of the converging premaxillaries. The nasals viewed from above are smooth, short, and broad. The *maxillaries* form a wide union with the frontals, and are deeply excavated behind the canines to the large infra-orbital foramina. The sutures of the *lachrymals* cannot be distinguished; they probably had a short exposure upon the face. The lachrymal foramen is within the orbit. The *frontals* are very long, extending from the interorbital space to the middle line of the cranium. There are no post-orbital processes, but rugose supra-orbital processes widely overhanging the orbits, which they completely conceal from above. They are separated by a notch from the prominent antorbital rugosity. The orbits are thus small and deeply enclosed. The *malars* have a faint postorbital process. Their greatest diameter is vertical, but the zygomatic processes of the *squamosals* are twisted, so that they unite with the

skull with the greatest diameter horizontal (Fig. 7). The squamosals are low and widely united with the parietals. The articular facets for the mandible and post-glenoid processes resemble those in the rhinoceros, on a larger scale. The *parietals* are rather short, a considerable portion of the cranium being formed by the *supra-occipitals*. The occiput is low and broad, with powerful condyles, which are much extended transversely. The space between the condyles and post-glenoid processes is rather short. The paroccipital and post-tympanic processes are on a level and closely united. The latter forms a wide union with the post-glenoid, completely enclosing the external auditory meatus inferiorly. The basi-occipitals and sphenoids form a prominent ridge, which is not overlapped anteriorly by the *pterygoids*. These bones are rather short and obtuse. This region of the skull is, upon the whole, very similar to that of the rhinoceros. The relations of the bones composing the hard palate are also rhinocerotic, except that the incisive alveolus is much shorter.

Dentition.

Lower Jaw. The crowns of the entire mandibular series are wanting. There were three *lower incisors*, which, so far as we can judge from the alveoli, were smaller than the upper, and much crowded by the large canines. The lateral incisor was the largest, the series decreasing towards the middle line. The *canine* fang is completely preserved, and indicates a large, semi-procumbent, laterally compressed tooth, measuring $1\frac{1}{4}$ inches in transverse diameter. It is followed by a diastema of two inches. The first and second *premolars* are wanting; the third has two fangs, and has about half the antero-posterior diameter of the first molar. The fourth premolar is two thirds the diameter of the first molar. The three molars increase rapidly in size, covering a space equal to that occupied by the upper molars, and three times that occupied by the premolars. The last molar is the largest, and was apparently trilobed.

Upper Jaw. The *maxillary* series are better preserved, the inner faces of the molar crowns showing on one side or the other in all except the first and last of the series. The *incisors* were placed in a uniform curvature, the lateral incisor being separated from the canine by a narrow diastema. The median alveolus is the largest, and the series apparently decreased in size laterally, reversing the relations of size shown in the mandibular series. The *canines* were subequal in size, and inclined forwards like those in the mandible. A narrow diastema separates this tooth from the small two-fanged second *premolar*, the first premolar having entirely disappeared. The third and fourth premolars have a broad, swollen, anterior transverse crest, and somewhat narrower and much more slender posterior crests. The fourth premolar has a faintly developed combing crest, as in the third premolar of *Amynodon*. The *molars* show a sudden and remarkable increase in size, occupying a space three times as great as that taken by the premolars. The crown of the first molar is transversely oblong, measuring $2\frac{3}{4}$ by 2 inches; the second is subquadrate; the third is antero-posteriorly oblong. As in the premolars, the anterior crest in m^1 and m^2 is the largest, and without distinct "anti-crochet," but the pos-

terior crest is also strongly developed. In its great inward extension m^1 has lost the internal cingulum, which is well developed in m^2 and m^3, as well as in the premolars. The broken outer contour of the molars indicates that the outline was similar to that observed in the *Amynodon* molars.

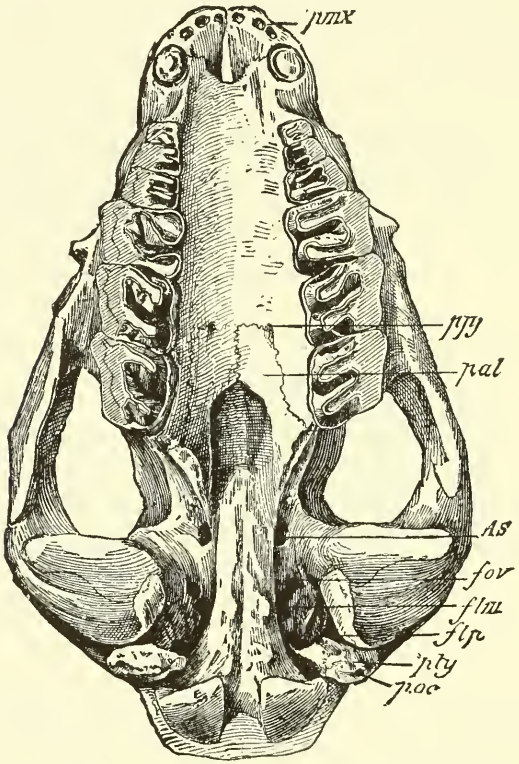


FIGURE 9. — Base of skull of *Metamynodon*. *ppf*, post-palatine foramen. *fov*, foramen ovale. *flm*, foramen lacerum medium. *flp*, foramen lacerum posterius. *As*, alisphenoid canal.

MEASUREM.

Skull.

	M.
Length of the skull from the incisor alveolus to the occipital condyles	.550
Transverse measurement, outside of the zygomatic arches	.365
Height of the occiput	.165
Breadth " "	.190
Length of face, front of orbit to premaxillaries, anterior border	.170
Length of cranium, front of orbit to occiput	.385

Upper Teeth.

	M.
Antero-posterior diameter of molar-premolar series (pm. .065, m. .160),	.225
Measurement of the canines, outside	.130
" " " inside	.056
Diameter of first molar, antero-posterior .047; trans.	.068
" third molar, " .060 "	.064
" fourth premolar, " .025 "	.045
" canine, " .035 "	.035

Lower Jaw.

Length of symphysis,	.130
Breadth of jaw opposite canines	.075
Diastema behind the canines	.050
Depth of jaw below first molar	.096
Antero-posterior diameter of molar-premolar series	.210
Measurement outside of the canines	.060
Transverse diameter of the canines	.030
Antero-posterior diameter of the canines	.037

RHINOCERIDÆ.

Aceratherium (Rhinoceros) occidentale, Leidy. This species is abundantly represented in the collection by skulls, teeth, and portions of the skeleton. Little more than the skull has been described as yet, but it is now possible to give a nearly complete account of the osteology of this species, as will be done in the final paper. The American species of *Aceratherium* are lighter, more slender, and retain more evidence of lophiodont ancestry than the European species, or any of the recent forms. The scaphoid does not cover the magnum so extensively as, and the lunar has a greater contact with the magnum than, in any of the modern genera, nor does the lunar rest so completely upon the unciform as in the latter. The metacarpals are heavier than in *Hyrachyus*, more slender than in the recent types; there were plainly four digits in the manus. The phalanges have about the same proportions as in the Sumatran rhinoceros. In the hind foot, compared with that of living species, we find that the tarsus is higher and narrower, the astragalus more deeply grooved, with longer neck and smaller cuboidal facet; the calcaneum is not so heavy; the metatarsals, especially the lateral ones, more slender.

In the limb bones the processes for muscular attachment, such as the deltoid hook of the humerus and third trochanter of the femur, are much less massively developed than in recent species.

HYRACODONTIDÆ.

Hyracodon nebrascense, Leidy. This species is very abundantly represented. Its osteology has already been partially described in another place,*

* E. M. Bull., No. 3, p. 17.

and it is therefore unnecessary to dwell upon it here further than to remark its very close resemblance in many important respects to the the eocene genus *Hyrachyus*. In general there are also certain analogies with the horse, in the delicate head, long neck, and elongated and narrow feet.

Hyracodon major, sp. nov. The type of this species is a fairly complete skeleton in the Princeton Museum, and in the Cambridge collection it is represented by a beautifully preserved fore-foot. Of this the carpus is high and narrow; the scaphoid is less produced laterally than in *Aceratherium*, the facet for the trapezium is very small and infero-lateral in position, those for the trapezoid and magnum much larger, and nearly equal in size. The lunar is contracted and anteriorly rests only upon the unciform, touching the magnum laterally, while in *H. nebrascense* there is apparently no anterior contact between the lunar and magnum. The cuneiform is high and much compressed, and the pisiform is short, compressed, and much expanded at the free end. The trapezium is a very small bone; it is pushed to the posterior side of the trapezoid so as not to be visible from the front, and has no contact with metacarpal II. The trapezoid is well developed, though relatively smaller than in the rhinoceros. The magnum is very large, in accordance with the development of the third digit, and is especially elongated in the vertical direction. The unciform is very high and narrow, and descends much below the level of the other carpals; owing to this compression the facet for metacarpal III. is entirely lateral instead of distal; there is an unusually extensive contact between the unciform and the magnum.

The lateral metacarpals are slender, narrow, and curved, the median one considerably longer and much heavier. Metacarpal II. abuts against the magnum by a considerable facet, while in *H. nebrascense* the facet is very small. Metacarpal V. is represented by a minute nodular bone, which is attached to the unciform and to the ulnar side of metacarpal IV.

Measurements.	*H. nebrascense.* M.	*H. major.* M.
Carpus, breadth	.040	.060
" height (median line)	.033	.050
Unciform, width	.020	.023
" height	.021	.033
Metacarpal II., length	—	.115
" III., "	—	.128
" IV., "	—	.105
" V., "	.010	—

Hyracodon (?) planiceps, sp. nov. This large species is distinguished from *H. nebrascense* by its extremely low and broad cranium, which is flattened upon the upper surface and entirely lacks the sagittal crest, which is represented by two ridges diverging from the supra-occipital border. This flattening alters the proportions of the occiput and temporal fossa. Comparing

this skull with that of *H. nebrascense*, we find about the same relative height as between the skulls of *Metamynodon* and *Amynodon*. The antero-external column is less sharply folded than in *H. nebrascense;* the first molar has a small conical tubercle at the entrance of the valley; the outer wall of the last molar extends beyond the posterior crest much more than in the other species of the genus, as in *Amynodon* and the *Lophiodontidæ*. The transverse crests are subequal and extend obliquely across the crown, thus differing from *H. arcidens*, Cope, in which the anterior crest is the longer and curves around the posterior.

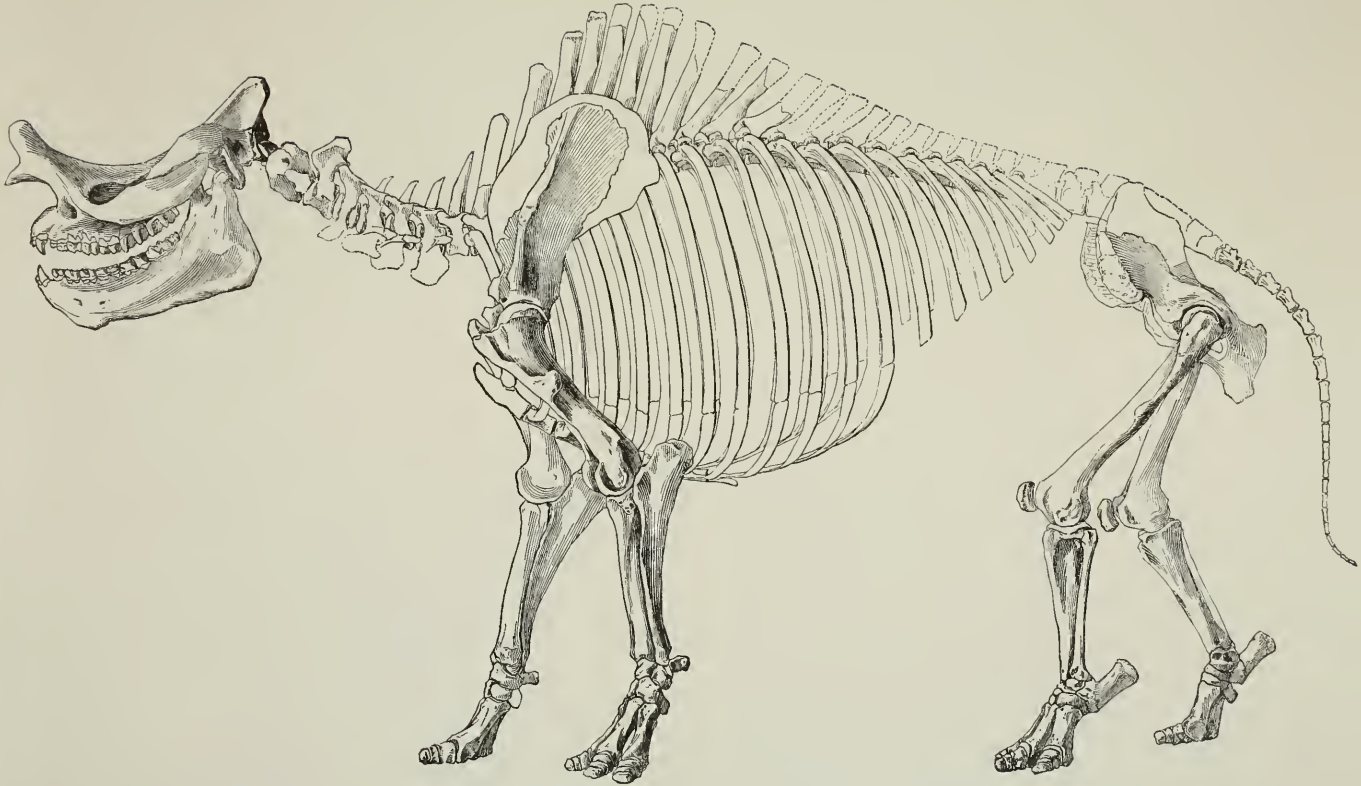
The skull, which was that of a young animal, lacks most of the facial portion. The extreme breadth across the zygomatic arches is $6\frac{1}{4}$ inches, while the height of the occiput is $2\frac{1}{2}$ inches; in a young specimen of *H. nebrascense* these measurements are $4\frac{3}{4}$ and 3 inches, a great difference of proportions. The periotic is exposed on the surface of the skull; the parietals are short; the post-glenoid and post-tympanic processes are separated below; the lachrymals extend considerably on the face.

Measurements.	*H. planiceps.* M.	*H. nebrascense.* M.
Upper molar series, length	.103	.070
First molar, width	.035	.026
Second " "	.036	.028
Third " "	.037	.026
Second molar, length	.035	.027
Third " "	.040	—

The proportions of the teeth thus differ considerably in the two species. In *H. planiceps* they increase in size from m. 1 to m. 3, while in the smaller animal m. 2 is the largest. In the former species the molars closely resemble those of *Amynodon*, but differ widely from the proportions found in *Metamynodon*. In fact, this animal may turn out to belong to a genus very different from *Hyracodon*, but at present we prefer to retain it provisionally in that group.

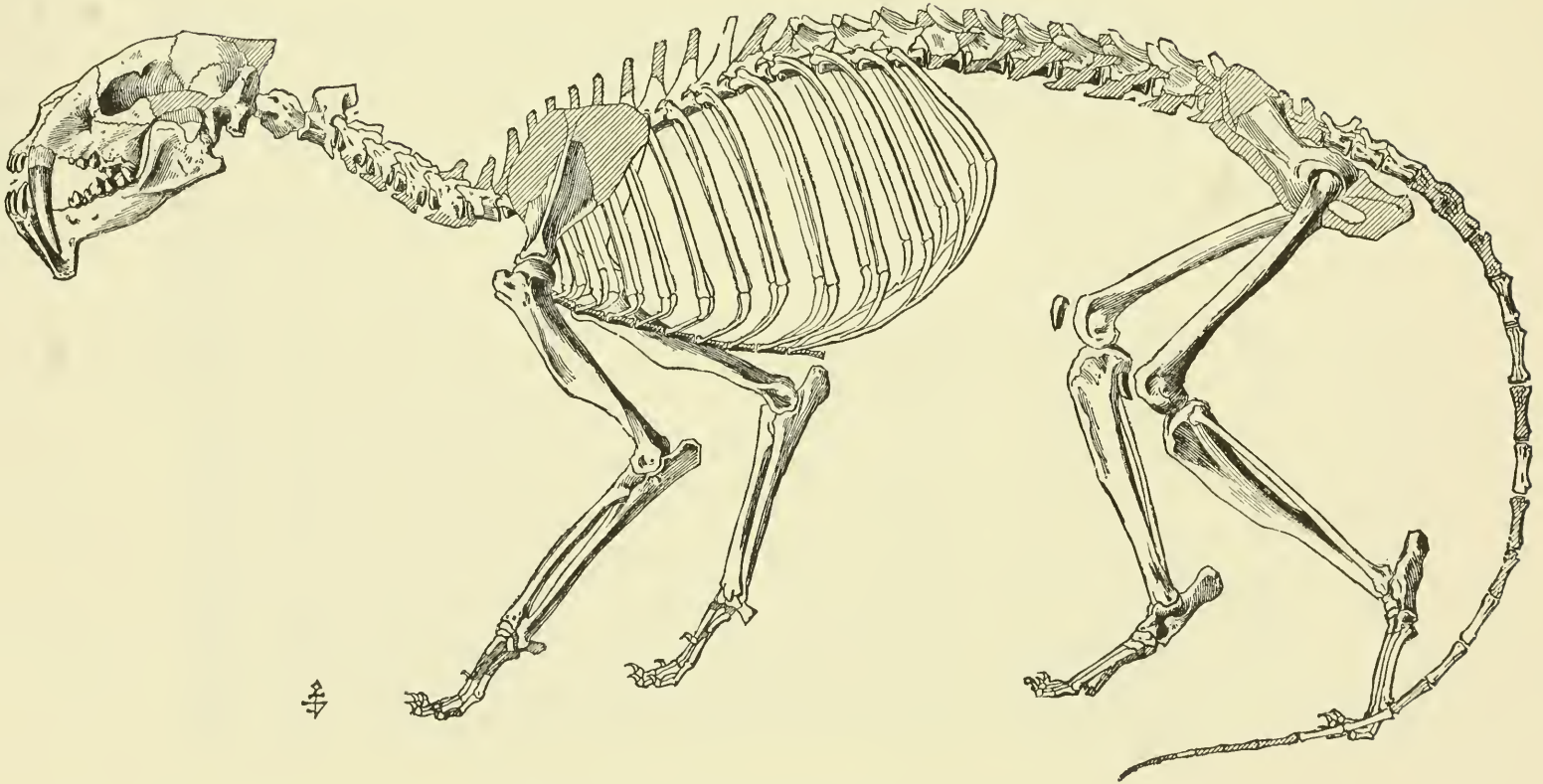
ANCHITHERIDÆ.

Mesohippus (Anchitherium) Bairdi, Leidy. The genus *Mesohippus*, Marsh, differs from *Anchitherium* in the structure of the incisor teeth, which have no enamel pit. The Cambridge collection contains an excellent skull and brain cast, the description of which is reserved for the memoir.



RESTORATION OF MENODUS PROUTII.

One sixteenth natural size.



RESTORATION OF HOPLOPHONEUS PRIMÆVUS.

One fourth natural size.

No. 6. *The Eyes in Scorpions.* By G. H. Parker.*

The subject discussed in the following pages has already attracted the attention of able investigators, and were it not that the authors of the later papers have pointed out questions only partially answered, a reconsideration of the subject might appear presumptuous. It is hoped that, in discussing these questions from an embryological as well as histological standpoint, the additional evidence obtained may throw some light on their solution.

The study of the eyes in Arthropods requires so much technical skill that until very recently satisfactory work in this field has been almost impossible. Aside from papers mainly of historical interest, the most comprehensive publication for the student to-day is Grenacher's "Untersuchungen über das Sehorgan der Arthropoden." This appeared in 1879, and contained an admirable study of the eyes in spiders; it did not, however, touch upon the organs of sight in scorpions. The same year, Graber, in his paper entitled "Ueber das unicorneale Tracheaten-Auge," severely criticised Grenacher's conclusions. Grenacher, in order to answer his critic, turned his attention to the eyes in scorpions, and, in his paper on the eyes in Myriapods, published in 1880, he included a reply to Graber. Three years later a comparison of the eyes in the scorpion and king-crab was published by Lankester and Bourne. The substance of these four papers, when viewed in the light of newly discovered embryological facts, has recently been fully discussed by Mark. Previous to the appearance of Mark's paper, Patten, after having made a comparative study of the eyes in certain mollusks and arthropods, included in his general description an account of the histology of the eyes in scorpions. The five papers quoted, namely, those of Graber ('79), Grenacher ('80), Lankester and Bourne ('83), Patten ('86), and Mark ('87), are the only ones in which the histology of the eyes in scorpions is considered.

The publications on the development of the eyes are even less extensive than those on the histology. Metschnikoff ('71, p. 225), in his

* Contributions from the Embryological Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the Direction of E. L. Mark. — No. XII. A Thesis presented for the Degree of S. B.

paper on the development of the scorpion, barely alludes to the eyes. Their probable method of development is described by Patten ('86, p. 672). His conclusions as far as they touch upon the eyes in scorpions are based upon inferences drawn from the method of development in other forms, not from actual observations. In a preliminary communication by Kowalevsky and Schulgin ('86, pp. 530–532) the method of development for the median eyes is described at some length. On account of incompleteness in their studies, these authors were forced to omit a description of the lateral eyes. Later in this paper, the substance of their communication will be considered.

The species of scorpions previously studied have been numerous. Graber ('79, p. 71) examined the eyes in *Scorpio europæus*, Schr., and *Buthus afer*, L. Grenacher's investigations ('80, p. 42) were made upon *Buthus afer*, *Ischnurus caudicula*, and *Lychas americanus*. *Androctonus funestus*, var. *citrinus*, Ehr., *Euscorpius italicus*, Roess. and *E. carpathicus*, were the species studied by Lankester and Bourne ('83, p. 180). The embryological researches of Kowalevsky and Schulgin were made upon *Androctonus ornatus*.

The species which I have studied belongs to the genus Centrurus.* In July and August, 1886, through Mr. C. W. Johnson, gravid females were obtained from Florida. At intervals during the following winter Mr. Johnson and Mr. F. S. Schaupp of Texas supplied me with fresh material. I am also indebted to Dr. H. A. Hagen for some alcoholic specimens from Arkansas.

In preparing the eyes for study by means of sections, the two chief difficulties encountered were the presence of chitinous lenses and dense pigment. It is difficult to cut the lens, and often this structure is in part torn away, thus destroying the surrounding tissue. In the median eyes, by careful dissection, the soft parts may be separated from the lens and cuticula, and cut without the interference of these hard structures. The separation is best accomplished after the tissues have been hardened. The method of dissection cannot be applied to the lateral eyes, for they are almost completely surrounded by chitine. In these eyes the best results were obtained by trimming off the chitine around the eyes, and cutting the retina and the lens after the removal of as much chitine as possible.

The pigment is so abundant and so dense that even the thinnest sec-

* I am unable to state what species this is. I have not succeeded in finding it described anywhere. Specimens in the collection of the Museum marked by Simon as "Centrurus sp. incog." are of the same species as those here described.

tions cannot be studied to advantage until they have been depigmented. For this purpose I know of only two classes of successful reagents, acids and strong alkalis. Grenacher has generally employed the first, Graber the second.

Of the acid reagents strong solutions are required. Lankester and Bourne ('83, p. 180) employed 5 or 10% solutions of nitric acid. In the eyes which I have studied, this mixture did not remove the pigment, even after the lapse of a week; and I was forced to use stronger and stronger grades, till 50% was reached. This mixture gives fair results, but must be made and used with much caution. A given volume of acid should be poured slowly into an equal measure of alcohol, never the reverse, and the mixture should be kept cool, otherwise the acid may attack the alcohol. In such an event the solution is rendered worthless, and, should the specimens be in it at the time, the heat generated by the reaction gives the acid such additional dissolving power that the sections are at once destroyed. A more efficient acid reagent is a mixture of equal parts hydrochloric and nitric acids. A 35% solution of this mixture in strong alcohol gives better results than the pure nitric acid at 50%, and does not so readily attack the alcohol.

Of the alkalis, weak ammonia, sodic hydrate, and potassic hydrate are most serviceable. The solids are to be preferred to the ammonia, since from them solutions of a definite strength can more easily be made. An aqueous solution of $\frac{1}{3}$ or $\frac{1}{4}$% potassic hydrate has given the most satisfactory results.

The method of using the depigmenting fluid is as follows. Unstained material is cut in paraffine; the ribbons are mounted on a slide with Schällibaum's fixative; when the sections are fixed, the paraffine is removed with turpentine; the slide with the sections is then successively washed with alcohol of 98%, 90%, 70%, and so on, till a grade homogeneous with the depigmenting fluid is reached. Into a shallow white dish filled with the depigmenting fluid the slide is now gently lowered. In a *few seconds* the pigment, dissolving, will be seen as a reddish cloud. The process is usually completed in less than a minute, and the slide is promptly transferred to a dish of clean water or alcohol and there gently rinsed. The sections are next stained by exposure to the dye in a shallow dish. After being sufficiently stained, they may be washed and mounted in glycerine, or, after the proper steps in dehydrating and clarifying, mounted in benzol-balsam or other mounting medium.

The dyes which have been found the most serviceable are some of the carmines and hæmatoxylin. The aniline dyes have almost invariably

given poor results. For general purposes Grenacher's alcoholic borax-carmine is excellent. In both embryonic and adult material Czoker's alum-cochineal gave fine nuclear outlines. In the adult eyes, the rhabdomes and the cell boundaries were most distinctly shown by Kleinenberg's hæmatoxylin. A very faint coloration with this dye gave the best results for nerve-fibres.

For the isolation of the retinal elements two maceration fluids were used. A weak solution of chromic acid, as employed by Patten ('86, pp. 736, 737), gave good results; but since the mycelium of a fungus is often developed in very dilute solutions of this reagent, it can be used only when it is carefully watched and its results are controlled by another method. It was employed in the following manner. The retina, after the removal of the lens and surrounding tissue, was placed for five or ten minutes in a $\frac{1}{5}\%$ solution. After this treatment, which slightly hardened the tissues, the first solution was replaced by a second of $\frac{1}{30}\%$. In this the retina remained for three or four days, at the end of which time the retinal cells were easily separable. The most satisfactory method of isolating the cells is to place on a slide in dilute glycerine a small portion of the macerated retina, and, having protected it with a cover-glass raised on wax feet, to gently tap the cover-glass till the cells are separated. One part of 0.2% solution of acetic acid in sea-water mixed with an equal volume of 0.04% osmic acid in sea-water, although only partially successful as a maceration fluid for the retina in scorpions, is a reliable check for the results obtained from chromic acid.

After the cells have been isolated, the abundance of pigment which they contain so obscures their contents that scarcely more than their outlines can be studied. The removal of the pigment is on the whole more successfully accomplished before than after isolation. For this process, as for simple isolation, the retina should be subjected to the action of $\frac{1}{5}\%$ chromic acid for five or ten minutes, and then transferred to a solution of $\frac{1}{3}\%$ potassic hydrate. In this the pigment dissolves, forming a reddish cloud. After about a minute the retina should be removed to distilled water, rinsed, and transferred to Grenacher's alcoholic borax-carmine. This reagent performs both the office of a maceration fluid and a dye. In from twelve to twenty-four hours the retinal cells can be isolated, and present in different regions of the retina three principal conditions. First, those from the exterior of the retina are seriously altered by the continued action of the potash; second, those from the centre of the retina remain almost unchanged, still retaining most of their pigment; third, those from an intermediate position, without being other-

wise much altered, lose most of their pigment. It is from these last that the best results were obtained.

The *eyes in scorpions* are situated on the prosomatic shield. According to their position they may be classed into two natural groups, the median and the lateral eyes. As their name implies, the median eyes are situated close to the sagittal plane. They are a little in advance of the centre of the shield, two in number, and always symmetrically placed. The lateral eyes form two isolated groups, one on either side, at the edge of the shield where its anterior border meets its lateral margin. In different genera, the number of eyes in each group varies from two to seven. Two kinds of lateral eyes have been distinguished; the larger or "principal," and the smaller or "accessory" eyes. As will be shown later, no essential difference exists between these two groups; the smaller and larger eyes are constructed on the same plan.

On account of the marked dissimilarity in the structure of the median and lateral eyes, they will be described separately.

The Median Eyes.

Grenacher ('79, p. 40) first pointed out that the vitreous and retinal layers in the eyes of spiders were separate. Graber in the same year confirmed this discovery, and showed that the median eyes of scorpions had a similar structure. These two-layered eyes were designated by Lankester and Bourne ('83, p. 195) as diplostichous, and among them were included the median eyes in scorpions. Up to this time all authors agreed that the median eyes of scorpions were two-layered.

One of the results of Locy's work ('86, p. 85), as Mark has indicated ('87, p. 71), is that in spiders the so-called diplostichous eyes are in reality three-layered, or triplostichous. The embryological facts on which this statement is based will be referred to later. For the present it is sufficient to note that an interesting question presents itself, namely, if the so-called diplostichous eyes in spiders have been shown to be triplostichous, may we not look for a similar condition in the median eyes of scorpions? Some of the reasons for believing this have already been stated by Mark ('87, pp. 55–58), but the final settlement of the question can only be reached through embryological means. It was my principal object in beginning these studies to reach a satisfactory conclusion in this matter.

Patten ('86, p. 672) had already claimed that the median eyes in

scorpions were three-layered, and that they were probably formed from a cup-like involution of ectoderm. The closure of the cup produced an optic vesicle, the deeper half of which became retina, while the more superficial half was probably represented by a structure to be described hereafter, the preretinal membrane. The details of this method of development, as will be seen later, are not confirmed by my observations; but nevertheless it remains to Patten's credit that he was the first to insist that the eyes in scorpions were three-layered, and not two-layered as had been previously held.

Metschnikoff ('71, p. 225), in his paper on the development of the scorpion, did not discuss the formation of the eye further than to claim for it a hypodermal origin. His evidence on this point can scarcely be considered as conclusive, for his studies were made from superficial views only.

The youngest material at my disposal was already somewhat advanced; but the eyes were still sufficiently undifferentiated to give adequate evidence as to their origin, and thus to afford a trustworthy basis for the interpretation of structures in the adult.

In the earliest stage examined, the eyes appear on surface view as a pair of oval, slightly pigmented areas. They are situated at the anterior end of the head, one on either side of the median line, and somewhat above the mouth. In a slightly older stage a sagittal section a little at one side of the median plane shows the region of the pigmented areas to be already composed of three layers of hypodermis (Pl. III. fig. 12, *pr r.*, *r.*, and *p r.*). The hypodermis of the prosomatic shield (*pr r.*) extends downward toward the mouth, and preserves its indifferent condition; before reaching that opening, it is folded upon itself, the deeper arm (*r.*) of the fold passing dorsally in contact with, the deep face of the external portion. The ventral third of the infolded layer is as thin as the external layer of hypodermis, but the remaining two thirds are considerably thickened and contain much pigment. This thickened layer, becoming rapidly thinner at its dorsal end, is also folded upon itself to form a third layer (*p r.*), which passes ventrally next the deep face of the thickened portion, and at the point of first folding becomes continuous with the external hypodermis as it proceeds in the direction of the mouth.

This condition is practically an involution of the hypodermis. The infolded layers take the form of a flattened sac, or pocket, the open end of which is situated in the median plane between the mouth and the previously described pigmented areas. From its opening the pocket extends vertically upward, and its anterior face is closely applied to the deep surface of the permanent hypodermis.

At the stage represented in Fig. 12, the cavity of the pocket is scarcely noticeable. It should appear, of course, between the second (*r.*) and third (*p r.*) layers, and at the deep end of the infolding a trace of it is visible (*cav.*). The second and third layers, however, are quite distinct, and show no indications of fusion. The cavity of the pocket is obliterated only by its opposite walls coming in contact, so that even in Fig. 12 a pocket may be spoken of without inconsistency. In stages earlier than that given in Fig. 12, the cavity of the pocket is very noticeable, and from its external opening to its deep end it is a continuous open space.

In a *horizontal* section of the earliest stage examined, the region just above the external opening of the pocket presents the appearance of a slightly irregular tube cut crosswise (Pl. III. fig. 13). The wall of the tube is made up of a single layer of hypodermis, whose deep surface is covered with a delicate basement membrane (fig. 13, *mb.*). The cavity of the tube is continuous with the pocket of the infolding (fig. 13, *cav.*). At about half the distance from its opening to its deep end, the pocket is divided in the median plane into a right and left compartment (Pl. III. figs. 14, 15). Each compartment has the form of a sac flattened from before backwards. The sacs extend dorsally on either side of the median plane, and end blindly.

One can distinguish, then, in the invagination a common neck, and two symmetrically placed sacs which arise from it. In the sagittal section (Pl. III. fig. 12) already described, the thin ventral third of the infolded hypodermis corresponds to the neck, and the thickened dorsal two thirds to the anterior wall of the sac. The position of the sacs is indicated externally by the areas of pigment already alluded to; the sacs are destined to become the retinas. The neck soon disappears, but some time before this takes place the outer wall of each sac is thickened still more and becomes more deeply pigmented. The thickened faces form the essential part of the retina, with which, after the closure of the pocket, the posterior thinner layer fuses.

The three hypodermal layers which enter into the composition of the eye, have received special names. That portion of the permanent hypodermis which is directly external to the optic sac, constitutes the first layer. At a later stage it produces the lens, and consequently has been termed by Mark ('87, p. 77) the "lentigen." By other authors it has been generally designated as the "vitreous." Directly under the lentigen, and forming the thick external wall of the optic sac, is the second or retinal layer. Behind this layer the thin internal wall of the sac forms

the third or post-retinal layer. At the sides and blind end of the sac, the two deeper layers, the retina and post-retina, are continuous.

Granting the optic sacs to have arisen by involution, it is important to notice that of the three layers described the retinal layer is inverted; i. e. that face which before involution is external becomes after involution internal. A similar inversion in the retinas of the anterior median eyes of Agelena has already been demonstrated by Locy ('86, p. 87). In fact, at this early stage, the only striking difference between the eyes in Agelena and Centrurus is, that in the scorpion the two sacs are united by a common neck, whereas in the spider they are independent involutions. It seems scarcely possible that this is an essential difference, and I therefore believe that the median eyes of scorpions, like the eyes of spiders, arise from hypodermal involutions not immediately connected with the formation of other organs.

Since the above conclusion was arrived at, Kowalevsky and Schulgin ('86, pp. 530–532), who have studied the development of Androctonus, have published in a preliminary communication the results of their work. In their description of the nervous system the development of the eye occupies several paragraphs. On account of the absence of figures their necessarily brief account is somewhat difficult to follow, and in one place I am not sure of their meaning.

Their statements on the median eyes are substantially as follows. A pair of semicircular depressions occur in the cephalic plate. From the anterior margin of each depression a fold grows down toward the mouth. The closure of each depression by its fold gives rise to a right and left cephalic vesicle. From the region at which the mouth of each vesicle has just closed, a new fold develops. Each of the new folds opens toward the animal's mouth, and takes on the form of a pocket. The right and left pockets thus formed are the first traces of the median eyes. The authors then describe the connection of the two pockets by a common neck, and the thickening of the retinal layer, in the ventral part of which pigment is deposited.

As will be noticed, the description summarized has to do with the earliest condition in the formation of the eye. The youngest stage of my material is too advanced to permit me to make positive statements on this subject. The point about which I have had difficulty relates to the description of the brain and eye folds. In describing the formation of the brain vesicles the authors speak of an *accessory fold* (eine accessorische Falte, p. 530). When the development of the median eyes is described, they speak of a *new fold* (eine neue Falte, p. 531). Finally,

in the paragraph especially devoted to the median eye (p. 531), the following occurs: "Die Mittelaugen werden von *der gleichen Falte** gebildet, welche am Baue der Kopflappen Antheil nimmt, nur mit dem Unterschiede, dass für den Bau des Hirns die tiefen Theile der Falte verwendet werden, während die Augen Derivate der peripherischen Theile *derselben Falte** sind." After speaking of an accessory fold and a new fold in connections already alluded to, the statement that the cephalic lobe and median eye are derived from the *same* fold seems to me contradictory.

The involution of the optic sacs in spiders, as Locy has shown ('86, Pl. XI. fig. 70), takes place at a much later period than the formation of the cephalic ganglia, and to all appearances independently of the latter. Whether in scorpions the growth of these two structures is connected or not, is a question for the determination of which I have not yet secured the requisite material. Besides the statements of Kowalevsky and Schulgin, which are somewhat obscure, there remains as a guide only the analogous case in spiders; the fact that the later stages in the eyes of spiders are essentially the same as those of the scorpion, lends support to the view that the eyes in scorpions, as in spiders, arise from folds independently of those concerned in the formation of the brain.

The most noticeable changes which the pair of sacs undergoes in the further development of the eyes are, first, an obliteration of their cavities, and, second, a considerable change in position. The closure of the sacs is first effected in the region where they unite with the common neck. From this point the fusion of the retinal and post-retinal layers proceeds toward the blind end of each sac, and the neck, becoming detached from the sacs, is slowly withdrawn to form a part of the permanent hypodermis (Pl. II. fig. 11, *col.*). The line of demarcation between the retina and post-retina at the deep end of the sac is the last trace of the already obliterated cavities (Pl. II. fig. 10, *cav.*).

The change in position undergone by the eyes is correlated with a change in the form of the animal's body. In the embryo the region of the prosomatic shield occupies the anterior face of the animal, and therefore lies in a plane approximately perpendicular to the long axis. The optic sacs are situated near the centre of this region, the plane of their flattening being nearly vertical, and the lines corresponding to the future axes of the eyes being horizontal. As the animal develops, the shield assumes a position more nearly horizontal, till at length it becomes entirely so. The axes of the eyes, having shifted through an arc of 90°,

* The Italics are not in the original.

then have a vertical direction. The only planes which in both the adult and embryo cut the eyes similarly are those parallel with the sagittal plane. In a horizontal section of a young embryo the eye shows the same relation of parts as one sees in a transverse section of an adult.

As previously stated, the eye in the embryo consists of three cell layers, lentigen, retina, and post-retina. These three layers are recognizable in the adult eye, and in considering the histology of this structure the three layers will be treated in the order named.

The *lentigen*, as Grenacher ('79, p. 40) first clearly demonstrated in spiders, is distinct from the retina, and is directly continuous with the hypodermis. Graber ('79, p. 61) established the existence of a similar condition in the median eyes of scorpions.

The lentigen results from a modification of the hypodermis directly external to each optic sac. For some time after involution this hypodermis consists of undifferentiated cells, whose positions are indicated by their spherical nuclei. About the time when pigment is deposited in the retina, the hypodermis in front of each pigmented area thickens, and the outlines of its cells become visible (Pl. III. fig. 15, *pr r.*). This is the first modification in the formation of the lentigen. The thickening of the lentigen increases, and each cell assumes the form of a long pyramid, whose base rests upon a membrane between retina and lentigen, and whose slightly truncated apex reaches the forming lens (Pl. II. figs. 9 and 10). In immature eyes the sides of the lentigenous cells are perpendicular to the surface on which they rest. In a transverse section of the head of an adult (Pl. I. fig. 2), the cells are curved. About three fourths of the lentigen, extending from the median toward the lateral margin of the eye, has its cells convex toward the sagittal plane; in the lateral fourth, the cells are concave toward the sagittal plane, and in the small intermediate region they are straight (compare Lankester and Bourne, '83, pl. X. fig. 8). In a longitudinal section of an adult head (Pl. I. fig. 1), the lentigenous cells all appear perpendicular to the surface on which they rest.

The nuclei of the lentigen cells, at the first indications of a thickening in the lentigenous region, keep to its deeper parts, and form in the adult eye a continuous line close to the deeper face of the lentigen (Pl. I. fig. 2, *nl. pr r.*).

The lentigen as a whole is of glassy transparency. In young stages the hypodermis at the edge of the lens nearest the median plane shows a deposit of pigment. This pigmented region in time extends around the

edge of the lens, and, as Graber has indicated ('79, p. 62), forms in the adult a complete circle, — the iris. In the iris proper the whole of each cell contains pigment granules, while in the adjoining hypodermis the granules are scattered in small groups through the cells, and are especially abundant at their outer ends.

The *lens* owes its origin exclusively to the activity of the lentigen. As is well known, it consists of a thickening of the external cuticula. The lentigen bears the same relation to the lens as the hypodermis does to the indifferent cuticula.

In Centrurus the cuticula at most points on the body consists of three layers. The outermost, first recognized as distinct by Graber ('79, p. 59), is a thin, homogeneous, colorless layer (Pl. I. fig. 2, *ll*). Under this is a second layer of about equal thickness with the first, but usually of a deep yellow color (Pl. I. fig. 2, *ll'*). These two layers together form about one fourth the whole thickness of the cuticula. The third layer (Pl. I. fig. 2, *ll''*), embracing the remaining three fourths, is distinctly laminated. The deepest lamella of this third layer readily takes up borax-carmine. The remaining lamellæ are distinguishable from the second layer chiefly by their want of color. The cuticula is very commonly penetrated by two sets of pore-canals (Pl. I. fig. 2, *can. po.* and *can. po.'*), fine and coarse.

As the indifferent cuticula passes into the region of the lens, the following conditions are noticeable. The external hyaline layer passes unchanged either in thickness or texture over the front of the lens. The second or colored layer becomes perfectly colorless, and by its increased thickness adds to the convexity of the lens. The bulk of the lens, however, is produced by a thickening of the third layer.

Whereas in the indifferent cuticula only its deepest lamella is colored with borax-carmine, in the lens all parts below the outer homogeneous layer readily take up this dye. A similar condition has been observed in several other local thickenings in the general cuticula, especially on the ventral side of the animal. The conclusion to be drawn from these observations is, that the lens in its composition is more closely related to the last-formed cuticular lamella than it is to the older lamellæ.

The coarse pore-canals never occur in the lens. Grenacher ('79, p. 90) was unable to find fine pore-canals in the lens of Phalangium, although Leydig had previously claimed them to be found in such lenses. Graber stated ('79, p. 60) that all arthropod lenses which he had examined contained fine pore-canals. In Centrurus, notwithstanding that many sections of lenses have been examined, fine pores have never been visible, although in the adjoining cuticula they are plainly evident.

Graber ('79, p. 59) raised the question whether the lens consists of only the normal cuticular layers thickened, or contains additional layers. This is a question upon which evidence is not easily obtainable, for it deals with layers which in the lens may be of considerable thickness and yet remain so thin as to be almost imperceptible in the indifferent cuticula. The condition of the lens in young individuals offers some evidence. About the time a young scorpion leaves the mother's back, the indifferent cuticula appears to consist conclusively of what in later stages corresponds to the external hyaline layer. Careful search has failed to show any subjacent cuticula, and yet in the region of the lens a very perceptible layer of stainable cuticula is visible. This seems to indicate that the lentigen has the power of producing cuticula independently of that produced by the indifferent hypodermis. Admitting this, it seems probable that of the many lamellæ in the lens some may be peculiar to the lens itself and unrepresented in the adjacent cuticula.

The separation of the retina and lentigen, as discovered by Grenacher, was further emphasized by Graber's discovery ('79, pp. 64–67) of a limiting membrane ("praeretinale Zwischenlamella") between them. This preretinal membrane, as Graber showed, is continuous with the "sclera" and the basement membrane of the hypodermis. The explanation of these structures which is offered by the formation of the eye from a hypodermal sac, has already been discussed by Mark ('87, p. 71). He has claimed that the sclera is the basement membrane of the post-retinal layer, and that the preretinal membrane is the fused basement membranes of the lentigen and retina. The explanation given in the case of the infolded eyes of spiders applies equally well to the median eyes in scorpions.

As to the nature of the basement membrane, especially in the region of the sclera and preretinal membrane, two opposing theories have been advanced. Graber ('79, pp. 63, 64) maintains that the basement membrane including the sclera is cuticular, not cellular, and as its matrix he claims cells whose nuclei were found both by Grenacher ('79, p. 60, fig. 34) and himself ('79, p. 64, fig. 18). For the preretinal membrane Graber ('79, pp. 64, 65) also claims a cuticular nature and states that it contains no nuclei. Lankester and Bourne ('83, p. 189) describe the ommateal capsule or sclera as laminate and devoid of nuclei. Mark ('87, p. 71) believes that the basement membrane with its modifications is a cuticula derived from the basal ends of the hypodermal cells.

Opposed to these views Schimkewitsch ('84, pp. 8, 9, 11, 12) maintains that the basement membrane and its modifications are connective

tissue, and consequently cellular. His first argument is for the basement membrane of the unmodified hypodermis. He shows that this membrane passes off from the hypodermis and invests muscles. Arguing by analogy from Froriep's conclusion that the sarcolemma of striate muscles in vertebrates is connective tissue, he maintains that the investment of the muscles in spiders and the continuous basement membrane are connective tissue. This argument of itself is scarcely convincing, for we do not know that the sarcolemma in vertebrates and arthropods has necessarily the same structure. Schimkewitsch used a second argument, which was more weighty, namely, that in the envelope of the eye (sclera) nuclei had been found. But the figures which illustrate this point are, as Mark ('87, p. 70) has stated, open to criticism.

In the developing eye in Centrurus, the basement membrane appears as a thin sharply defined structure bounding the deep ends of the hypodermal cells. It is continuous over the optic nerve, and unites with the membrane investing the brain (Pl. III. fig. 16, *mb.*). In the region of the preretinal membrane it is double, one layer limiting the lentigen, the other the retina (Pl. II. fig. 9, *mb.*). This confirms Mark's theoretic conclusion. In the earliest stages studied, mesodermic nuclei occur at intervals between the two membranes, except directly over the centre of the eye, where the two membranes are in contact (Pl. III. figs. 14, 15, *nl. ms d.*). Although mesodermic nuclei occur between the two retinas, and also between the retina and the brain, they are never found within the basement membrane of the eye region, as they are within the envelope of the brain. As the two layers of the preretinal membrane unite, the mesodermic cells, instead of being included between them, migrate toward the margins of the eye, and leave the preretinal membrane when completed destitute of cellular elements. In the region of the sclera, however, mesodermic nuclei, often very much flattened and always closely applied to the outside of the membrane, are distinguishable almost up to the adult state (Pl. III. fig. 15, Pl. II. fig. 9, *nl. ms d.*). It is, therefore, nearly certain that some of the substance of this mesodermic covering enters into the formation of what is known as the "sclera." In the adult sclera, however, no nuclei are visible, and besides it is by no means certain that these mesodermic cells form a continuous investment over the basement membrane, — perhaps nothing more than a network.

The nuclei in the eye on the right of Schimkewitsch's Figure 11 (Pl. III.) are almost identical in appearance with those found in the young eyes of Centrurus, where they *appear* to occupy the middle of the membrane; they are in reality outside it, as can be readily demonstrated

when, as sometimes occurs, one finds a place where the mesodermic element with its nucleus has been loosened from the sclera, and both nucleus and sclera remain uninjured.

The nuclei which Schimkewitsch has drawn in Fig. 4 (Pl. II.) and Fig. 11 (Pl. III.) are undoubtedly mesodermic, and represent a thin tissue on the outside of the sclera.* Those in his diagramatic figure (Pl. III. fig. 4), if they are, as Schimkewitsch says, identical with those of the other two figures, are mesodermic nuclei drawn on the wrong side of the sclera; if, on the other hand, their position is correct, they are not the same nuclei as those in Figs. 4 and 11, but, as Mark ('87, p. 70) maintains, the nuclei of the post-retinal layer.

From what has been said it will be inferred that in the adult neither the sclera nor preretinal membrane contains nuclei. It is conceivable that in some cases mesodermic nuclei might be surrounded in either of these structures. Such, of course, would be exceptional. Of the twenty preretinal membranes studied in section only one has shown nuclei; but, strange as it may seem, half † of this one contained no less than fourteen. They were uniformly distributed, and always elongated parallel to the striations of the membrane. In position they were appreciably nearer the retina than the lentigen (Pl. II. fig. 8, *nl. ms d.*). This instance shows that the preretinal membrane may at least have a central layer of mesodermic tissue, although the greater part of it is ectodermic cuticula.

The great thickness of the preretinal membrane in scorpions has already been noticed by Graber ('79, p. 67). In Centrurus, as in others, it presents a fibrous laminate appearance, and in specimens treated with potassic hydrate it is slightly swollen and vacuolated.

At the edge of the preretinal membrane, where its two constituents separate, the one which passes around the retina is much thinner than the one which continues under the hypodermis. This is an indication of the relative amount of substance contributed respectively by the retina and the lentigen in the formation of the membrane. The line which would separate the lentigenous from the retinal part must be drawn somewhat nearer the retina than the lentigen. It is on this line, more-

* This limitation of the meaning of the word "sclera" seems desirable in view of the possibility that a mesodermic covering may be altogether wanting, but it is not intended as a criticism of Schimkewitsch's statement that the sclera contains nuclei; for the "sclera" as previously understood may evidently be in part mesodermic, and therefore cellular, as Schimkewitsch has claimed.

† The remaining half of this membrane was mounted on a second slide, and treated by a method which did not make its nuclei distinguishable.

over, that one would expect to find mesodermic elements if any were present, and naturally enough it is in this region that the exceptional nuclei previously referred to occur (Pl. II. fig. 8).

The fact that mesodermic tissue is incorporated in the preretinal membrane makes it highly probable that the mesodermic cells noticed on the sclera really contribute to that layer, and that the sclera is in part mesodermic and in part ectodermic. To summarize, then, the preretinal membrane, like all parts of the basement membrane, appears first as an ectodermic cuticula. Mesodermic elements may be included between its two layers, but this is the exception. The most of the membrane is in any event cuticula, of which the greater part is produced by the lentigen, the lesser by the retina.

The *retinal* and *post-retinal* layers. — The intimate connection into which these two layers enter in forming the retina is a sufficient reason for considering them together. Grenacher's ('79, pp. 39–57) researches on the eyes of arachnids led him to believe that the retina consisted of a number of similar elements, each of which contained a rod-like body, or bacillus, and a nucleus. Each element was, therefore, to be considered a single cell. He also discovered that there were two different types in the disposition of the nucleus and bacillus. Either, as in the anterior median eyes of Epeira ('79, pp. 43–45, fig. 18 A), the bacilli were in front of the nuclei, or, as in the posterior median eye (fig. 18 B), they were behind the nuclei. In the structure of the eye this interesting dimorphism, as Grenacher has termed it, has proved to be a feature of common, if not universal, occurrence with spiders.

Graber, who based his conclusions on the study of the retina in scorpions as well as spiders, opposed Grenacher's views, and claimed to have found in the median eye of Buthus ('79, pp. 71, 72) at least two nuclei to each element, — a large, basal, ganglionic nucleus, and, near the outer end of the element, a smaller apical one. The equivalent of Grenacher's bacillus lay between these. In the case of the lateral eyes * of Buthus (Pl. V. fig. 5), as well as in the anterior and posterior median eyes of Epeira (Pl. VII. figs. 25, 26), Graber figured a third small nucleus directly behind the bacillus.

This discovery, if corroborated, would invalidate Grenacher's view of dimorphism in the eyes of spiders, and one would be forced to admit that the retinal elements are multinuclear, and therefore not single cells. Grenacher's ('80, pp. 415–430) reply to Graber, at least so far as the

* When the discussion of the lateral eyes is reached, the subject of their nuclei will be considered more at length.

retina in scorpions is concerned, is based on a study of the median eyes only. He ('80, pp. 422–425) shows conclusively that for a ganglionic nucleus Graber has described and figured a body which is not a nucleus. Grenacher, after a careful search for Graber's middle and anterior nuclei, positively denies their existence. This, as Grenacher says, leaves the retinal elements in scorpions devoid of nuclei; he then proceeds to show that in the region of Graber's so-called ganglionic nucleus there exists a true nucleus essentially unlike the latter. Therefore, according to Grenacher, the retinal elements in scorpions are to be placed in the category to which the anterior median eyes of Epeira belong.*

Lankester and Bourne ('83, p. 188) agree with Grenacher that each retinal cell contains a single nucleus; but they also maintain that Graber's anterior and middle nuclei are to be found in the retina. These nuclei, however, do not belong to the retinal elements proper, but to small intrusive pigment cells.

The composition of the adult retina in Centrurus has been studied by means of sections and maceration preparations. A horizontal section of an adult retina (Pl. I. fig. 1) presents a concavo-convex outline; a portion of the convex face occupies the median plane of the body, and is fused to the corresponding part of the opposite retina. The concave face is limited by the preretinal membrane. The concave region is composed of a series of deeply pigmented club-shaped masses, which taper off into the lighter middle region. Behind the lighter area, which occupies fully half of the thickness of the retina, many of the bands and lines of pigment become thickened into irregular dark blotches, which make up a poorly defined mottled area. This soon merges in the median plane into the retina of the opposite side, and elsewhere into a densely pigmented zone limited behind by the sclera. This pigmented zone can be traced around the side of the retina till at the edge of the latter it becomes confluent with the pigmented area first mentioned.

After removing the pigment and staining the section in Grenacher's alcoholic borax-carmine, the outermost pigmented region (Pl. I. fig. 2) is seen to consist of a very granular substance, in which cell-walls can be traced from the preretinal membrane backward to the pointed, rod-like structures, or rhabdomes. The latter cause the lightness of the large

* Graber ('79, p. 69) designated those elements in which the nuclei were behind the bacillus as "post-bacillar"; those in which the nucleus was in front of the bacillus, "pre-bacillar." Mark ('87, p. 73) has proposed for these terms pre- and post-nuclear, respectively. Since these present advantages over the older terms, they will be adopted in the following pages.

middle area. This granular substance (Pl. II. fig. 4) extends down between the rhabdomes, and merges with a less regularly granular substance behind. The rhabdomes at their deep ends merge imperceptibly into this irregularly granular substance. In the region where the deep ends of the rhabdomes disappear, large slightly granular nuclei occur (Fig. 4, *nl. r.*). All the nuclei in the retina of Centrurus are found in what has been described in the pigmented eye as the mottled area. The nuclei nearest the concave surface of the retina are the largest, and, as has been previously mentioned, are slightly granular. Behind these, in the middle of the nuclear region, smaller oval nuclei (Fig. 4, *nl. pig.*) occur. Here also nerve fibres are abundant, and those curious bodies mistaken by Graber for nuclei and designated by Lankester and Bourne under the name of phaospheres (Fig. 4, *pha sp.*). The deepest nuclei (Fig. 4, *nl. p r.*) in the retina are flattened, and more deeply colored than the rest. They lie upon the internal surface of the densely pigmented zone, previously mentioned, and form a line of separation between that zone and the coarsely granular substance in front. The substance of the deepest zone is almost identical in character with that of the outer portion of the retina, and its granular appearance, like that of the external layer, is largely due to the colorless remains of pigment granules. The smaller anterior and median nuclei of Graber do not exist in Centrurus, either *in* the retinal cells or *between* them, as claimed by Lankester and Bourne ('83, pp. 192, 193). The latter authors state ('83, p. 192) that the reason Grenacher overlooked these nuclei was that the acid which he used to remove the pigment destroyed them. In the case of Centrurus sections depigmented with the 35% mixture of nitric and hydrochloric acids, with ⅓% solution of potassic hydrate, or *unaffected* by depigmenting reagents, but colored with borax-carmine and cut three micromillimeters thick, show no trace whatever of anterior or middle nuclei. The examination of fresh material and of maceration preparations has given the same results. Moreover, since the nuclei in the brain after treatment with ⅓% potassic hydrate are not to be distinguished from those in the same organ unaffected by that reagent, it seems scarcely possible that the same reagent could *destroy* nuclei in the retina. It is therefore safe to conclude that at least in the retina of Centrurus no nuclei exist external to the band of larger nuclei already described.

Having shown that the retinal nuclei are limited to the deeper region of the retina, and that these nuclei are of three principal types, we are now prepared to inquire into the cellular composition of the retina. This is best done by means of isolation preparations. In the retina

there are at least three kinds of cells. Two can be readily isolated; the third has been studied only in sections.

The retina extending from the line of deepest flattened nuclei to its outer margin breaks up into two very distinct forms of cells, — retinal or nerve-end cells, as Lankester and Bourne ('83, p. 182) have called them, and pigment cells. The retinal cells (Pl. II. fig. 5) are elongated and rounded at their outer ends; they terminate below in nerve fibres. From the rounded external end the calibre is uniform till the region of the rhabdomeres is reached. Here the cells increase in diameter, and then continue for some distance uniform in size. Finally, each cell, enlarging slightly at its deep end, rapidly tapers into a nerve fibre. Throughout its whole extent the retinal cell contains pigment, which is principally concentrated, however, at its rounded outer end.

The pigment cells (Pl. II. fig. 6) at their anterior ends, like the pigmented tops of the retinal cells, abut against the preretinal membrane. From this they pass backward, and in the region of the rhabdome, where the retinal cells enlarge, they contract to thin fibres, which, after the rhabdome has been passed, again expand into irregular pigment sacs at the deep part of the retina. When isolated, they present the appearance (Pl. II. figs. 6, 7) of two sacs of pigment connected by a slender rigid fibre.

The large round or slightly oval nuclei have been identified as belonging to the retinal cells (Pl. II. fig. 7), and the smaller oval nuclei occupy the deep swollen ends of the pigment cells. It is possible that some of the pigment cells may not be prolonged in front of the rhabdomes, and therefore not possess anterior sacs; but I have never been able to discover such. The filamentous middle portion connecting the two extremities of the long pigment cells is so constant and characteristic in maceration preparations, that pigment cells which do not extend to the front of the retina must form the exception, if in fact they exist at all.

Another method employed in studying the cells of the retina, and one especially instructive for the region of the anterior zone, was by the aid of sections perpendicular to the retinal cells. The retina has the form of a shallow bowl; consequently in sections perpendicular to its axis the deeper portions of the retina will lie at the periphery of the section, and its centre will be the region nearest the preretinal membrane.

Figure 3 represents a portion of a retinal section whose centre, and consequently highest portion, is toward the right, and whose periphery or deeper portion is toward the left. The relatively higher portion of the

section is at that point below the preretinal membrane where the rhabdomeres diminish into simple cell boundaries, and the five cells which make a single group are here easily distinguishable. To the left the rhabdomes are much larger, and have assumed their usual outlines. The rhabdomes have increased in size at the expense of the cells. It will be noticed that each of the cells present belongs to some group of rhabdomeres, and consequently *all* are retinal cells.

The section (Fig. 3, *a*) which was the next external to the one just described shows practically the same condition, except that, being slightly nearer the front of the retina, the rhabdomes are not quite so distinct, especially in the extreme right, where in one or two groups scarcely any trace of the rhabdomeres can be seen. Nevertheless, all the cells of the former section can be identified, and moreover between the groups in the upper right hand corner an additional cell is noticeable. This cell, which by a comparison of the two sections is seen to be a supernumerary element, is not a retinal (nerve-end) cell; but since in maceration preparations the outer expanded ends of the pigment cells were always found near the preretinal membrane, there is every reason for considering this such a cell. Moreover, when sections nearer and nearer the preretinal membrane are examined, these additional cells become more numerous, until finally they are with difficulty distinguished from the retinal cells. The anterior sacs of the pigment cells, then, can be demonstrated on sections as well as by maceration.

The rhabdomes never reach the anterior face of the retina, but fall short of it by the thickness of several sections. This space between the rhabdomes and preretinal membrane corresponds to the anterior zone of deep pigmentation seen in longitudinal sections. The pigment in this region is so dense that the outlines of the cells can be traced only with difficulty.

The phaospheres, as Lankester and Bourne ('83, pp. 185, 186) have called the curious bodies mistaken by Graber for nuclei, are abundant in the nuclear zone of the retina (Pl. II. fig. 4, *pha sp.*). They are as small as the oval nuclei around them, and often smaller, but differ from these in containing usually one, and sometimes two, three, or even four highly refractive dots. Lankester and Bourne state that they are usually behind the nucleus of the retinal cell. In isolated cells I have never succeeded in satisfactorily identifying them, therefore in Centrurus I cannot feel sure of their position. In one section only has a phaosphere occurred in a prenuclear position; in all others they have been strictly behind the neighboring nuclei.

As to their nature two suggestions have been made. Lankester and Bourne ('83, pp. 185, 186) imply that they are of the nature of rhabdomes; in this light they are further discussed by Mark ('87, p. 93). Patten ('86, p. 684) is inclined to look upon them as degenerate nuclei. In Centrurus the phaospheres, being of nearly the same size as the nuclei, present less favorable opportunities for study than in those scorpions where they are much larger. Those in Centrurus stain in much the same way that the surrounding nuclei do, and in fact are to be distinguished from these mainly through their highly refractive dots. In many cases, however, these dots are not well marked, and it is then difficult to determine whether a given body is a nucleus or a phaosphere. The nuclei are constantly oval in form; the phaospheres are more or less irregular in outline. This irregularity, however, is only noted in phaospheres which have very refractive dots, and never in those which seem to be transitional in form between nucleus and phaosphere.

The third type of cell occurs as a single layer of pavement-like elements at the back of the retina (Pl. II. fig. 4). It has been correctly stated by Graber ('79, p. 84) that this pavement layer is the matrix of the sclera. Lankester and Bourne ('83, p. 192, pl. X. fig. 8, *p*) have also observed it in Androctonus, where the cells are relatively much smaller than in Centrurus. In sections of Centrurus the outlines of these cells are visible, though faint; in form they are broadly columnar. Their nuclei, as previously stated, take a deep color, are flattened, and are always located at the end of the cell farthest from the sclera.

This deep layer of cells envelops the convex face of the retina, passing up on its sides till it reaches the edge of the retinal cup (Lankester and Bourne, '83, pl. X. fig. 8, *p*). Here, as Graber has shown ('79, Pl. V. fig. 14), it becomes continuous with the retinal layer. Only in the region where the retinas of the two median eyes fuse does this basement layer fail to cover the deep surface of the retina proper.

The principal histological changes which take place during the development of the eye relate to nuclei, the pigment, and the optic nerve. The formation of the optic sacs, the disappearance of their common neck, and the fusion of the post-retinal with the retinal layer has already been described.

While the eye is yet an ectodermic pocket (Pl. III. figs. 12–15), the *nuclei* are distributed through the whole of the thickened retinal layer; in the post-retina they form a single row. At this stage the nuclei of the different cells are indistinguishable. Their outlines are round or

slightly oval; their contents, except for a few sharply marked granules, are very transparent. Somewhat later, but before the optic sacs have closed, they are less abundant near the front face of the retina, but otherwise no special arrangement is as yet evident.

The rhabdomeres play an important part in the future distribution of the nuclei. They first appear as light streaks, which, beginning close to the preretinal membrane, gradually extend backward. With the extension of the rhabdomeres, the nuclei recede to the deeper parts of the eye, and with very few exceptions* never occupy a place in front of the rhabdomeres.

At about the time the young scorpion is born, the cavity of the optic sac having disappeared, the nuclei of the retinal layer are found to have arranged themselves in two groups. In axial sections of the eye (Pl. II. fig. 9) one group forms an irregular line at the base of the rhabdomeres, the other a broad band in the deeper part of the eye. The space separating these two groups is considerable, and contains only a few scattered nuclei. The deeper nuclei in the broad band, i. e. those nearer the sclera, are to be referred to the post-retinal layer.

At this stage the nuclei are still undifferentiated, and even after the young scorpion has left the mother's back it is some time before one can recognize differences between them. It is only in the fully developed adult that a marked differentiation is reached. By this time the nuclei of the retinal cells have become slightly more homogeneous (Pl. II. fig. 4, *nl. r.*) and somewhat reduced in size. The nuclei of the post-retinal cells have become much flattened and stain more deeply. These, as well as the nuclei of the pigment cells, are reduced in size, and have become more homogeneous. The columnar "matrix" cells previously described, and to which these flattened nuclei belong, constitute the post-retina; and their transition at the rim of the optic cup into the retinal layer is only a preservation of the relation they have sustained to that layer from the time of the original involution. This interpretation of the "matrix" cells has already been maintained by Mark ('87, p. 56).

The phaospheres appear at a very late date. In young scorpions which have left the mother's back no trace of phaospheres was discoverable, and it was only in those eyes in which the three forms of nuclei were already distinguishable that the structures were noticed. The time of their appearance — a period of nuclear differentiation — is evidence in favor of their nuclear origin.

* In only one instance out of the many in which developing eyes have been examined has a nucleus remained in a prebacillar position.

That the retinal cells and the post-retinal cells, as well as the pigment cells, *contain* pigment, has already been stated. Lankester and Bourne ('83, p. 194) were somewhat in doubt whether the retinal cells in the median eyes of scorpions contained any pigment. Patten ('86, p. 728) believes that they do not contain pigment. The evidence furnished by sections perpendicular to the length of the cells (Pl. II. fig. 3, *gra. pig.*) is, I think, conclusive.

Under the head of "intrusive pigmentary connective tissue," Lankester and Bourne ('83, p. 191) include the pigment cells in Androctonus, and, with less confidence, their so-called intracapsular pavement. The pigment cells proper are considered by them as of mesodermic origin. This they defend by several arguments, but admit that their reasons cannot be regarded as offering a sufficient basis for a final conclusion.

During early stages in the development of Centrurus, mesodermic tissue is often seen making its way into the substance of the brain, and its appearance is characteristic. It penetrates into the nervous system as thin continuous sheets of cells, which in cross-section appear as lines. During the development of the eye no such appearances have been encountered, and it is fair to conclude that mesodermic tissue has not gained access to the eye by the same means that it has to the brain.

Lankester and Bourne suggest that it may have entered the eye capsule at the opening for the optic nerve; but the capsule (sclera) is reflected on to the optic nerve, and, even admitting that mesodermic tissue did gain access here or from the brain, where it undoubtedly exists, one would naturally expect the pigment to appear first in the region of the optic nerve. Contrary to this, as Kowalevsky and Schulgin ('86, p. 531) have shown, — and my own observations confirm theirs, — pigment first appears in the front of the retina on its ventral — afterward becoming its anterior — edge, at a point farthest from that where the optic nerve joins the retina. Taking all the evidence into account, it seems that the nerve-end cells, the intracapsular pavement cells (post-retina), and the pigment cells are alike ectodermic, and that the retina contains no tissue that can be referred to a mesodermic source.

The *optic nerve* in the adult scorpion joins the eye at a point on the under side of the eye capsule. From this point bundles of fibres pass anteriorly through the base of the retina in front of the post-retinal layer, and from small secondary bundles are given off single fibres which join the *bases* of the retinal cells.

In the youngest stages studied, the optic nerve was already formed, and its fibres (Pl. III. fig. 17, *n. fbr.*) passed over the front of the retina,

apparently connecting with the *external* ends of the retinal cells. At least the fibres disappear here, and cannot be traced into the retina. The optic nerve (Pl. III. fig. 16, *n. opt.*) at this stage emerges from the retina by passing over the rim of the optic cup in a region corresponding to the outer edge of the pocket. The region extends from the dorsal margin half-way down toward the ventral margin of the cup.

During the further development there is but little change in the point of exit for the optic nerve. It simply shifts from its posterior lateral position in the embryo, to a posterior ventral one in the adult. The change in the course of the intracapsular fibres is much more significant.

There is reason to believe that in the embryo the nerve fibres are attached to the *external* ends of the retinal cells (Figs. 14–17). In the adult they certainly emerge from the *deep* ends of these cells. The steps which connect the earliest with the final condition consist of a migration of the point of attachment for the nerve fibre from the external end of the cell to the deep end. The migration of the fibres takes place at the same time that the nuclei recede into the deeper parts of the eye, and seems to be controlled by the same influence, namely, the growth of the rhabdomeres. An analogous condition in the eyes of Agelena has been described by Mark ('87, pp. 84–87). There is, however, a difference; the nerve fibres in Agelena never come to have a post-nuclear attachment to the retinal cell, whereas in the figures of Graber and those of Lankester and Bourne, and certainly in the retina of Centrurus, the nerve fibres emerge from the cell behind the nucleus. Mark ('87, pp. 91, 92) has claimed for these facts an important significance, and concludes that they point to a functional condition of the retina before involution. The bearing of this will be further considered under the head of theoretic conclusions.

The Lateral Eyes.

The lateral eyes in scorpions, although in some respects more interesting than the median eyes, have on the whole received less attention. Grenacher in his two papers previously quoted makes no mention of them; for our present knowledge of their structure we are indebted to the researches of Graber ('79) and of Lankester and Bourne ('83). The results of these inquiries are in so far unsatisfactory that in several essential points they are directly opposed to each other. The points upon which there is a conflict of opinion are (1) the origin of the retina, and (2) the presence or absence of a lentigen.

On the question of the origin of the retina in arthropods, two unreconcilable opinions have been held. Some authors have maintained that the retina was an outgrowth from the brain, and others that it was a modification of the hypodermis. Graber may be taken as a representative of the former school, Grenacher of the latter. The evidence upon which they based their opinions was derived in the two cases from quite different kinds of eyes. Grenacher believed, since he had found in eyes like those of the larval Dytiscus a retina which was continuous with the hypodermis, that therefore the retina in the more complex eyes was derived from the same hypodermal source. Graber, arguing from those eyes in which the retina is separated from the hypodermis by a preretinal membrane, maintained that the retina is an outgrowth from the brain, and not derived from the hypodermis. Such an eye as the larval eye of Dytiscus would, even in the absence of other evidence, seriously weaken the force of Graber's argument. As an explanation of such structures, Graber is inclined to think that the larval eye of Dytiscus really possesses a preretinal membrane, with hypodermis in front of it; but that, on account of the thinness of this structure, Grenacher has overlooked it. In other words, Graber considers the arthropod ocellus as a two-layered structure, the outer layer of which is hypodermal, and the inner layer, or retina, neural in its origin.

In Graber's figures and description of the lateral eye in scorpions, the two essential parts of the median eyes, the lentigen and retina, are represented; but the lentigen, unlike that of the median eyes, is reduced to a very thin layer of cells. This is perfectly consistent with Graber's theory; but whether it represents the actual structure of the eye or not is questionable, since Lankester and Bourne ('83, pp. 182 and 187) expressly state that the lateral eye of Androctonus is composed of a single layer of cells, — a thickening of the superficial hypodermis, — and claim that Graber is incorrect in describing a separate layer concerned in the formation of the lens.

Since the publication of these papers, Locy's discovery of the method of development in spiders' eyes has firmly established the hypodermal origin of the retina. It has also offered a perfectly rational explanation for the presence of Graber's preretinal membrane. Thus the hypothesis of the neural origin of the retina is no longer tenable.

The presence or absence of a *lentigen* and preretinal membrane is, as Mark ('87, p. 55) has stated, important in determining whether a given eye has been formed by involution with inversion or not. Although the hypodermal nature of the retinas in both the lateral and median eyes of

scorpions is unquestionable, yet whether the lateral eyes, like the median, have been formed by an involution with inversion, or whether their formation is accompanied simply by a thickening and more or less extensive depression in the hypodermis, is still an open question. Graber's figure ('79, Pl. V. fig. 4), with its preretinal membrane and lentigen, would indicate that the eye arose by involution. Lankester and Bourne's figures ('83, Pl. X. figs. 2, 3, and 4), in which these structures are absent, would favor the explanation that the eye is only a hypodermal thickening.

The position of the lateral eyes in scorpions has already been described. In the adult Centrurus each group consists of four eyes, three of which are large and are designated by systematists as "principal" eyes, and the fourth is small and known as an "accessory" eye. The larger eyes are arranged in a horizontal line at the antero-lateral angle of the shield; the small eye is above a point midway between the posterior and middle larger eyes.

A vertical section through the axis of one of the larger eyes (Pl. III. fig. 18) shows at the surface a strongly convex lens (*lns.*) beneath which a relatively small retina (*r.*) appears. The outline of the latter is marked by the basement membrane (*mb.*), and on its dorsal and ventral edges it is seen to be continuous with the hypodermis (*hd.*). In an eye from which the pigment has not yet been removed, the whole retina is intensely black. The pigment extends up to the margin of the lens, as figured by Lankester and Bourne ('83, Pl. X. fig. 1), and spreads out above and below into the adjacent hypodermis. It is far more abundant in the dorsal hypodermis than in the ventral.

The *lens* in the adult eye consists of essentially the same parts as in the median eye, and contains no pore-canals. Its substance except the front hyaline layer is stained throughout by alcoholic borax-carmine. In young individuals (Pl. III. fig. 21) the lenses of the lateral eyes, even better than those of the median eyes, show a formation of stainable cuticula (*ll''*) under the hyaline layer (*ll*) before a similar secretion has taken place from the general hypodermis.

In the adult eye not the least appearance of a *lentigen* or preretinal membrane is to be found, even after careful depigmentation. The fact that the pigmentiferous tissue extends up to the lens is of itself suggestive of the absence of a lentigen, for in ocelli generally this layer is remarkable for its transparency. When to this is added the fact, that no nuclei exist in the front part of the eye, and that in no place does the basement membrane extend as a preretinal membrane across the front of

the eye, the evidence against the presence of a lentigen is apparently complete.

The composition of the *retina* in the lateral eyes is much more difficult to study than in the median eyes. This is due in part to the small size of the lateral retinas, and in part to their almost complete chitinous investment. To make isolation preparations is wellnigh impossible, by far the best results being obtained from the study of sections.

Graber ('79, Pl. V. fig. 5), believing that the composition of the median and lateral retinas was essentially the same, has figured in the lateral eyes of Scorpio retinal elements with three nuclei. Moreover, the retinal elements are grouped, as in the the median eyes, in fives (Pl. V. fig. 8).

Lankester and Bourne ('83, pp. 181–187) claim that the retina consists of unicellular elements, or nerve-end cells, as they call them, and of indifferent cells. The indifferent cells occur both *between* the nerve-end or retinal cells, as "interneural cells," and *around* the edge of the retina, as "perineural cells." The indifferent cells all contain pigment; the retinal cells, in their opinion, are probably pigmented on their peripheries.

In Centrurus the nuclei (Pl. III. fig. 18, *nl. r.* and *nl. pi n.*), as in the median retinas, are limited to the deeper portion and to the periphery of the eye, and Graber's anterior and median nuclei are not present. The nuclei (*nl. r.*) belonging to the deep portion of the retina are slightly larger than those (*nl. pi n.*) on the periphery, and very uniform in size. The fact that in this part of the retina there is only one form of nucleus leads to the conclusion that the retina in Centrurus is composed of only one kind of cells, and that here the interneural cells described by Lankester and Bourne do not exist.

Sections perpendicular to the axis of this retina show immediately under the lens the sharp outlines of cells which deeper in the retina have their walls thickened into rhabdomeres. No additional cells, like those in the median eyes, appear in the outermost sections of the retina, and therefore the interneural cells, if present, must be limited to the deeper portion of the retina. The fact that there is no difference in the nuclei of this region leads me to believe that interneural cells are entirely wanting. In Centrurus the retinal cells (Pl. III. fig. 19) show no tendency to be arranged in groups of five, and the rhabdomeric thickening (*rhb m.*) takes place on all sides of the cell. This is particularly noticeable in examining the region nearest the lens. In the outermost sections the cells are sharply outlined and their walls are very thin. In the second or third section from the lens, the walls suddenly become

thicker around the whole circumference of the cell, and take on a lustrous appearance. With Kleinenberg's hæmatoxylin the substance of the rhabdomeres can be colored, and the line of demarcation between products of the separate cells can be distinguished. This structural condition can be traced to the deeper part of the retina, where the cell outlines become indistinct, the rhabdomeres incasing each retinal cell for a half or two thirds of its length.

Pigment (Pl. III. fig. 19, *gra. pig.*) is uniformly distributed through the retinal cells, as well as the perineural cells to be described later. This is best seen in sections perpendicular to the axis of the eye. Phaospheres, although present in the median eyes, do not occur in the lateral eyes. The optic nerve (Pl. III. fig. 18, *n. opt.*) emerges from the deep end of the retina, and its course is so oblique to the axis of the eye that a section which shows the retina well seldom shows much of the optic nerve.

The perineural cells surround the depressed retinal area, and their attenuated ends, especially on the ventral side of the eye, often reach out, even in the adult condition, in front of the retinal cells themselves (Pl. III. fig. 18). The positions that the nuclei occupy in the ventral portion of the perineural ring suggest that these cells may at one time have extended far enough to have completely covered the retina, and the fact that in young individuals (Pl. III. fig. 21) the retina is largely covered by the perineural cells indicates that in all probability the lens is the product of these cells. In that event the perineural cells are the physiological equivalent of the lentigen. The peripheral margin of this lentigenous ring passes by insensible gradations into the surrounding hypodermis.

The *development of the lateral eyes* is referred to by Kowalevsky and Schulgin ('86, p. 531) as follows: "Die Seitenaugen entwickeln sich unabhängig von den Mittelaugen, und bei ihrer Ausbildung nimmt die Vertiefung der obern Schicht der Kopfplatte Antheil. Die Einzelheiten dieses Vorganges sind von uns noch nicht bearbeitet." This is the only reference which they or other students have made to the development of the lateral eyes.

The "ocular areas," as Lankester and Bourne designate the regions occupied by the lateral eyes, appear in Centrurus as pigmented tracts of hypodermis on either side of the head and a little below and behind the median optic sacs. Horizontal sections of the embryo cut these areas in the most advantageous way for a general study; they show that the whole ocular area is produced by a thickening of the hypodermis.

The horizontal sections shown in Figs. 22–27 (Pl. IV.) are arranged to represent the characteristic features of the ocular area of the *left* side of the head, as one would observe it in passing from a dorsal to a more ventral position. Calling that of Fig. 22 the first section, they are the 1st, 3d, 6th, 13th, 16th, and 21st sections in a series from a single animal. Fig. 22 represents the hypodermis directly above the eyes and at the edge of the ocular area. The extent of this area is indicated by the thickened region. Two sections below this (Fig. 23) the ocular area is more extended, and shows a single simple depression (No. 1). It will be observed that the band of nuclei indicates a more marked depression even than the outline of the hypodermis itself. This simple depression in the hypodermis indicates the position of a lateral eye. The cells which compose the wall of the cup are wedge-shaped; their nuclei are below the middle of the cells, and those cells which occupy the central portion of the depression are so attenuated at their free ends as scarcely to reach the surface. The basement membrane (*mb.*) closely invests the deep face of this structure, as it does any ordinary hypodermal thickening. The sixth section, Fig. 24, exhibits a region in which the ocular area is greatly thickened, but it shows no depressions, and the nuclei extend very near to the surface. Fig. 25, seven sections deeper than Fig. 24, presents four cup-shaped depressions (Nos. 2, 3, 4, 5), each essentially like the depression previously described. The two central depressions (Nos. 3, 4) are the largest; next in size is the anterior one (No. 2), and smallest of all is the posterior one (No. 5). As in the case of depression No. 1 (Fig. 23) the band of nuclei in the region of each depression forms a much deeper cup than the outer surface of the hypodermis. The basement membrane (*mb.*), as in Fig. 23, invests only the deep surface of each hypodermal cup. From this plane ventrally the hypodermis gradually becomes thinner, and at the extreme edge of the dorsal shield the indifferent hypodermis is reached. (Compare Figs. 18, 20.)

The five depressions just described are early stages in the development of the lateral eyes. In the adult Centrurus only four eyes are present. Of the five depressions seen in the embryo the most posterior (No. 5) of the ventral four disappears, and three remaining form the "principal" lateral eyes. The fourth or "accessory" eye arises from the dorsal depression (No. 1), which, even in the embryo, occupies a position above the space between the second and third depressions (Nos. 3 and 4) of the lower row. The presence in the embryo of a rudimentary fifth eye is interesting, in view of the fact that there are five eyes in the *adult* of Androctonus, as has been shown by Lankester and Bourne. It is proba-

ble that one of these five eyes in Androctonus is represented by the rudimentary eye in Centrurus, although this can be definitely settled only by a careful comparison.

In the embryo the fibres of the optic nerve (*n. opt.*) emerge from the *base* of the retina (Pl. IV. fig. 25). This, moreover, is their position throughout the life of the scorpion (Pl. III. fig. 18).

The further changes which affect the form of the optic depressions before they become matured eyes are unessential modifications of the already established plan. At the time of the production of a lens (Pl. III. fig. 21) the lentigenous (perineural) cells stretch over from all sides and overtop the retina. The external ends of the lentigenous cells contain no pigment (Pl. III. fig. 20).

The basement membrane, from the time when the depressions are formed till the eye is completed, covers the modified hypodermis as it covers a simple hypodermal thickening. There is never any indication of a preretinal membrane, nor, from the structure of the eye, should we expect to find one. In all stages the basement membrane presents the appearance of a single delicate lamella, and at no time is there an additional sheet of mesodermic tissue, as in the median eyes.

The evidence derived from the anatomy of the adult eye, the absence of a preretinal membrane and permanent lentigen, and the continuity of the retina with the hypodermis, together with the facts derived from a study of the development of the eye, show conclusively that in scorpions the retina of the lateral eye is what Lankester and Bourne have called monostichous, and that this retina, unlike that of the median eyes, is normal, not inverted.

Theoretic Conclusions.

The striking similarity in the structure and development of the median eyes in scorpions and the anterior median eyes in spiders has already been indicated. In both cases the retina by a process of involution has become inverted. The question whether the retina was functional during the phylogenetic involution of the eye is, as Mark has maintained, answered in the affirmative by the phases noted in the development of the optic nerve. At least, the fact that the fibres of the optic nerve are at first attached to the morphologically deep ends of the retinal cells, and only at a later date come to emerge from the opposite end, is most easily explainable on the supposition that the retina was functional before involution. The primitive eye would, then, consist of a single layer of retinal

cells from the deep ends of which the nerve fibres emerge. Admitting that in the ancestral eye the rhabdomeres were in their usual position, namely, at the outer end of each retinal cell, an inversion of this retina would not only place the optic fibres on the front face of the retina, but the rhabdomeres would come to occupy the deep ends of the cells. The prenuclear rhabdomeres of a normal retina would, therefore, be homologous with the postnuclear rhabdomeres of an inverted retina. The prenuclear rhabdomeres of the median eyes in scorpions must, then, be secondary structures, developed in such a way as to replace functionally the older postnuclear structures.*

The phaospheres, as Mark ('87, p. 93) has already suggested, may represent the remains of postnuclear rhabdomeres. These are to be regarded, then, in the nature of disappearing organs, and the fact that in some species of scorpions they are present, while in others they are absent, would favor this view. As Mark has stated, the phaospheres, if they represent postnuclear rhabdomeres, should be found only in eyes with inverted retinas. Lankester and Bourne, as previously mentioned, have described them in the lateral eyes of Euscorpius. Mark hesitated, in the case of the lateral eyes, as to whether he should follow Graber's observations and consider them triplostichous, with inverted retinas, or whether he should follow Lankester and Bourne and consider them monostichous. In the former case the phaosphere might readily represent postnuclear rhabdomeres ; in the latter, this interpretation would be out of the question. In Centrurus the structure and development of the lateral eyes show conclusively that they are monostichous, and there seems to be small room to doubt that the same is the case with the lateral eyes in Euscorpius. In these eyes, however, Lankester and Bourne claim the presence of phaospheres. I have had no material from Euscorpius to examine ; but since in Centrurus the median eyes contain phaospheres, while the lateral eyes are devoid of them, it is a matter of interest to see whether, upon further investigation, the presence of phaospheres in the lateral eyes of Euscorpius is confirmed, or whether that genus, like Centrurus, has phaospheres in the median eyes only. If they should not be found in the lateral eyes, there would still be reason for considering them the remnants of rhabdomeres; but if they should be found there, this view would be no longer reasonable.

The possible relation of the median to the lateral eyes in scorpions has already suggested itself, for in pointing out the probable nature of

* This relation of the structures of the normal and inverted retina has been fully discussed by Mark ('87, pp. 87–94).

the phylogenetic antecedent of the median eyes, a condition has been implied which agrees with the essential features of the lateral eyes. Of all the eyes in spiders and scorpions, the lateral eyes in scorpions are undoubtedly the least complicated, and they may be looked upon as deviating least from the probable ancestral type.

Summary of Results.

Nos. 2–11 refer to the median eyes; Nos. 12–17 refer to the lateral eyes.

1. The *retinas* of the median and lateral eyes are strictly *hypodermal* in their origin.
2. The *median eye* is *triplostichous*, and is formed by an involution of hypodermis accompanied with an *inversion* of the middle layer, which forms the retina proper.
3. The first layer or *lentigen*, is modified hypodermis immediately external to the pocket of involution, and, in addition to secreting the lens, serves a purpose which gave to it its earlier name of "vitreous."
4. The *lens* is the specialized cuticula produced by the lentigen. It differs from ordinary cuticula in containing *no* pore-canals, and, excepting the external hyaline layer, in being stainable throughout.
5. The *lentigen* can produce cuticula independently of the general hypodermis.
6. The second layer, or *retina*, is inverted, and consists of two kinds of cells, — retinal (nerve-end) cells and pigment cells. It contains phaospheres.
7. The *retinal* (*nerve-end*) *cells* contain pigment; their walls are thickened into prenuclear rhabdomeres, and a nerve fibre emerges from their deep ends. They are so arranged in groups of five, that five rhabdomeres are united to form one rhabdome.
8. Each of the *pigment cells* is reduced to two sacs, connected by a stiff fibre. The external sac contains pigment; the internal, the nucleus and pigment.
9. The third or *post-retinal layer* is the "sclera matrix" of Graber. It becomes intimately fused with the retina.
10. The fibres of the *optic nerve* in the embryo emerge from the external ends of the inverted retinal cells; in the adult, from the opposite ends.

11. The *basement membrane* is a cuticula produced by the inner ends of the hypodermal cells. The *preretinal membrane* is the united basement membranes of the lentigen and retina. It may or may not contain mesodermic elements. The *sclera* is the basement membrane of the post-retina. It is usually overlaid with a delicate mesodermic tissue.
12. The *lateral eyes* are *monostichous*, and arise from a simple thickening and depression of the hypodermis.
13. A ring of "*perineural*" *cells*, forming the margin of the depression, secretes the lens, and therefore constitutes the lentigen. Since, owing to subsequent recession, they do not remain interposed between the lens and retina, they have not the double function of lentigen and "vitreous" which the outer layer of the median eye has.
14. The *lens* has the same structure as in the median eye.
15. The *retinal cells* occupy only the deeper portion of the depression. There are no interneural cells. Along the external portion of each retinal cell its lateral walls are thickened into rhabdomeres. The nucleus is near the deep end of the cell, and from this end the nerve-fibre emerges. Phaospheres are not present.
16. The *basement membrane* (sclera) contains no mesodermic elements. There is no preretinal membrane.
17. The *lateral eyes* may be fairly taken to represent the *ancestral type* of the *median eyes*.

CAMBRIDGE, July 1, 1887.

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EXPLANATION OF FIGURES.

ABBREVIATIONS.

a.	Anterior.	*n. fbr.*	Nerve fibre.
can. po.	Fine pore-canals.	*n. opt.*	Optic nerve.
can. po.'	Coarse pore-canals.	*nl. ms d.*	Nucleus of mesodermic cell.
cav.	Cavity of infolding.	*nl. pig.*	" pigment "
cl. pig.	Pigment cell.	*nl. pi n.*	" perineural "
col.	Neck of invagination.	*nl. p r.*	" postretinal "
enc.	Brain.	*nl. pr r.*	" lentigen "
env. em.	Embryonic envelop.	*nl. r.*	" retinal "
gra. pig.	Pigment granule.	*p.*	Posterior.
h d.	Hypodermis.	*pha sp.*	Phaosphere
ir.	Iris.	*p r.*	Post-retina.
ll.	Outer hyaline layer of cuticula.	*pr r*	Lentigen.
ll'.	Middle " " "	*r.*	Retina.
ll''.	Deep " " "	*rhb.*	Rhabdome.
lns.	Lens.	*rhb m.*	Rhabdomere.
mb.	Basement membrane.	*scl.*	Sclera.
mb. pr r.	Preretinal "	1, 2, 3 4 5.	Lateral eyes.
mu.	Muscle.		

All the figures were drawn with the aid of an Abbé camera. Except where otherwise specified, all the preparations were examined in benzol-balsam.

Figures 1 to 18 represent the structure of the *median* eyes. Figures 1 to 9 illustrate the *adult* eye.

PLATE I.

Fig. 1. A horizontal section of the retinas of the two median eyes seen from the dorsal side. The tissue has been simply hardened and cut, the pigment remaining intact, and no dye being employed. ×195.

Fig. 2. A transverse section of the retina of the right median eye seen from the posterior face. The pigment has been removed by potassic hydrate and the tissue stained in Grenacher's alcoholic borax-carmine ×195.

PLATE II.

Fig. 3. The outer face of a frontal section through the retina of a median eye. The portion of the figure nearer the right side is close to the centre of the retina, that to the left is nearer the periphery. Colored with Klei-

nenberg's hæmatoxylin. The outline figure on thin paper (Fig. 3a) is taken from the section directly external to the one just described. ×475.

Fig. 4. Posterior face of a part of a transverse section of the retina described in Fig. 2. ×475.

Fig. 5. A retinal cell isolated in $\frac{1}{50}$% solution of chromic acid, and examined in a mixture composed of equal parts of water and glycerine. ×475.

Fig. 6. A pigment cell isolated and examined in the same manner as that shown in Fig. 5. ×475.

Fig. 7. A retinal cell with an attached pigment cell. The pigment was removed with a solution of potassic hydrate, and the cell was isolated and stained in Grenacher s alcoholic borax-carmine. Examined in a mixture of glycerine and water. ×475.

Fig. 8. The posterior lateral portion of a horizontal section of a retina seen from the dorsal side. Partially depigmented with a solution of potassic hydrate, and subsequently stained with Czoker's cochineal. In several places the lentigen has been artificially ruptured. ×475.

Figs. 9 to 17 represent the structure of the median eyes in young scorpions.

Fig. 9. The posterior face of a transverse section of the right retina in a young scorpion about the age at which it leaves the mother's back. Depigmented with potassic hydrate; stained in Czoker's cochineal. ×195.

Fig. 10. The left face of a section through the right eye parallel to the sagittal plane. Pigment unchanged; stained in Grenacher's alcoholic borax-carmine. This specimen was taken about the time of birth. ×195.

Fig. 11. Right face of a section from the sagittal plane of an individual somewhat younger than that seen in Fig. 10. In this section the neck of the invagination (*col.*) is seen to reach almost to the retina. In the sections on either side of this the neck appears much reduced, and at no point does it unite with the retina. ×195.

PLATE III.

Fig. 12. The right face of a section almost in the sagittal plane of an embryo. The lower part of this section was exactly in the median plane. The upper part was somewhat to the right of that plane. Pigment unaffected; stained in Grenacher's alcoholic borax-carmine. ×195.

Figs. 13 to 17 represent the dorsal faces of a series of horizontal sections in the region of the median eyes. In all the pigment is unchanged, and all have been stained with Grenacher's alcoholic borax-carmine. The region of the eye extends through forty-four sections. ×195. Beginning with the most ventrally situated and passing dorsally, Fig. 13 represents the seventh. It will be noted that the sections are not strictly horizontal, but that they dip slightly to the left; consequently in Fig. 13 the wall of the pocket is cut on the right in the thickened or retinal region, but on the left nearer the orifice of the pocket.

Fig. 14, the fourteenth section, shows the cavity of involution just before it is divided into a right and left compartment.

Fig. 15, the twenty-third section, shows the cavity divided.

Fig. 16, the thirty-first section, shows the right compartment reduced in size.

Fig. 17, the forty-first section, represents the wall of the deep (dorsal) end of the pocket cut tangentially.

Figs. 18 to 27 inclusive relate to the structure of the *lateral* eyes. Figs. 18 and 19 are from preparations of adult eyes.

Fig. 18. The anterior face of a vertical axial section of the right eye (No. 2); compare Pl. IV. Depigmented with a solution of potassic hydrate; stained with Grenacher's alcoholic borax-carmine. × 325.

Fig. 19. Anterior face of a frontal section. Partially depigmented with potassic hydrate; stained with Kleinenberg's hæmatoxylin. × 475.

Figs. 20 to 27 inclusive give the structure of the eyes in young scorpions. Figs. 20 and 21 are from material of the same age as Fig. 9.

Fig. 20. Anterior face of a vertical axial section of left eye (No. 3). The pigment is unaffected, and no dye has been used. The edge of eye No. 1 is seen above. × 325.

Fig. 21. Anterior face of a vertical axial section of left eye depigmented in potassic hydrate and stained with Grenacher's alcoholic borax-carmine. × 325.

PLATE IV.

Figs. 22 to 27 inclusive are taken from the dorsal faces of a set of sections of the youngest embryos at hand (of the same age as those from which Figs. 13 to 17 are taken). The sections have been depigmented with a solution of potassic hydrate and stained in Grenacher's alcoholic borax-carmine. × 325. The figures represent the left cluster of lateral eyes. Beginning dorsally and proceeding ventrally, Fig. 22 is the first section, Fig. 23 the third, Fig. 24 the sixth, Fig. 25 the thirteenth, Fig. 26 the sixteenth, and Fig. 27 the twenty-first.

1.
a
p
prr
ml prr
mb prr
ins.
2
can.pó.
can.po.
ll.
ll'
ll''
hd
scl
rhb
pr

gra.pig
3.
hh
mh.pr
8
prr.
mh
sel
nl.ms.d
4
mh
prr
9
hd
phar.p
nl.ms.d
gra.pig
pr.r
10.
cav
5.
6
7.
hh.m
11.
mu

13
mb
cav
14
prv.
cav
enc
15.
nl mxd
cav
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17
prr
n fbr
enc.
nl mxd
12
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16.
gra ptg
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19
rhbm
gra ptg
20
r
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18
r
mb
lns.
21
n opt.
n opt
nl prn
hd
r
vl r
prr

25
n opt
mb
n opt
mb
mv.em
24
al.med
mb
mv.em
22.
mv.em
mb
mv.em
al.lat.
mv.em
26.
27
mv.em
mb
mb
23
al.med
mb
mv.em

No. 7. — *Studies from the Newport Marine Zoölogical Laboratory. Communicated by* ALEXANDER AGASSIZ.

XIX.

On Certain Medusæ from New England. By J. WALTER FEWKES.

THE following paper is intended as a contribution to our knowledge of New England jelly-fishes. It deals for the most part with animals of this group from the northern waters of the coast of Maine, and from Grand Manan.* During a vacation visit of a month's time at the latter locality, in the summer of 1886, the author collected several new and highly interesting medusæ.† Incidentally, in studies of animals of other groups in the summer of 1885, some observations were made on Eastport medusæ.

* While the waters of the Gulf Stream justly attract the attention of naturalists interested in the study of our pelagic fauna, there is much yet to be done with the dip-net in the cold waters of the Bay of Fundy and the coasts of Nova Scotia and New Brunswick.

† Mention is made in these pages of those medusæ only which were collected by the author, and no attempt is made to include all those mentioned by others.

It is next to impossible to make out a complete faunal list of the medusæ of any locality, except after years of study. From the nature of their life, stragglers and sporadic swarms of rare medusæ appear in localities where the medusan fauna has been well studied. For ten years I have kept watch of the medusæ which appear in Narragansett Bay in summer months, and a season rarely passes in which some jelly-fish new to the known fauna is not observed. Sometimes specimens of some new genus will appear in such abundance that it seems impossible that we could have missed seeing them if they had appeared in other summers. In some years the water near the Newport Laboratory is filled with Pleurobrachiæ, while in others stragglers only appear. In the past summer the most common acaleph in Narragansett Bay was Dactylometra, hundreds of specimens of which were seen, and yet in former summers we rarely have observed more than a half-dozen in the course of a summer.

In the light of these facts it seems preposterous to attempt a monograph of the medusæ of the Bay of Fundy with the limited material collected on the short visits which I have been able to make to these waters.

I have had in mind since that time a new visit to these localities to gather materials for the publication of a monographic paper on the medusæ of the Bay of Fundy, but have been unable to make the necessary collecting trips for its completion. It is now thought best to publish some of the more interesting observations which have already been made, as aids to those who may make a more exhaustive local study of these animals, or as a preliminary to a more extensive examination of animals of this group from these localities.

While the majority of the medusæ here mentioned are from Eastport, Maine, and Grand Manan, New Brunswick, a description of a new genus, Hydrichthys, from Newport, R. I., is added.* This strange genus is parasitic in its hydroid stage on the sides of an osseous fish, and besides the unique parasitism presents us the anomalous condition of an attached hydroid closely related to the well-known Velella and Porpita. The form of Nanomia, the anatomy of Callinema, and the peculiarities of the various other medusæ here mentioned from the vicinity of Grand Manan, show how characteristically boreal this medusan fauna is, and how much it differs from that of Narragansett Bay. They show how rich the field is for an extended research in this region in this kind of marine study.†

The short visit which was made to Grand Manan, and the collecting trips to Eastport in 1885 and 1886, have shown me that the medusan fauna of the Bay of Fundy and Passamaquoddy Bay, near these places, is very characteristic. It differs markedly from that of Newport, and is distinctly boreal in its affinities. While this paper was in preparation the author has had occasion to study the medusan fauna of the Arctic Ocean, and to publish notices of jelly-fishes collected by Lieutenant Ray and General Greely in high latitudes. It has been noticed in carrying on this work simultaneously that there is a marked similarity in the fauna of the Arctic and that of the Bay of Fundy, and it may be said that the

* This curiously modified hydroid was captured during the summer session (1887) of the Newport Marine Laboratory.

† The author would here add a notice of his own experience to that of others as to the advantages of Grand Manan for marine zoölogical work. While many, perhaps a majority, of those who have studied zoölogy in this place, have spoken of its many advantages for dredging and shore collecting, few have tried surface fishing in these waters. I had been led to suppose from certain sources, that revelations with the Müller net would be small in these localities, but I find Grand Manan and Eastport among the best localities which I have visited on the New England coast for the collection of pelagic and "surface animals" with the dip-net.

relationship is closer between the jelly-fishes of these distant localities than between those of Narragansett Bay and the Bay of Fundy. The cause of this similarity may readily suggest itself to one who examines the direction of the currents of water which bathe the New England coast. The cold currents setting down from the Arctic have brought with them an assemblage of medusan genera of a facies in marked contrast with that of those brought into Narragansett Bay by warmer waters. This assemblage partakes of the characters of the Arctic, where the current has its birth. While it is true that some of the northern and boreal genera of medusæ occasionally round Cape Cod and appear even in numbers in the bays to the south of this headland, they show by their rarity, and their dependence upon the prevailing winds at the time, that their home is to the north.*

Among familiar examples we might mention the well-known *Cyanea arctica* and *Aurelia flavidula*. Hardly a summer passes in which both of these genera are not found in Narragansett Bay near the Newport Laboratory, and sometimes the former are in great numbers. I have, however, never seen them at Newport so large or so numerous as those which were taken almost every day at Eastport. Sporadic examples of Turris, Melicertum, and Staurophora are constantly taken in our surface fishing at Newport, but a few days at Eastport showed me a wealth of individuals of these genera which was unknown to me before. This difference in fauna exists also in the Physophores. Nanomia never ventures into Newport waters, and the magnificent Agalma seems to have its habitat on our coast limited to the southward of Cape Cod.

If it were the purpose of this paper to contrast the pelagic medusan faunæ of the Bay of Fundy and Narragansett Bay, many other instances might be mentioned to show how different the jelly-fishes of the two

* While there are many boreal medusæ which straggle into Narragansett Bay, a still larger number of those whose home is in the tropics make their way into our Southern New England waters through the agency of the Gulf Stream. The surface waters of the Gulf Stream are often blown nearer shore than is commonly supposed. I have noticed in the water near the Laboratory a rise in temperature of over ten degrees in a single flood of the tide. The higher temperature of the water is a good sign that we are to expect oceanic animals in our dip-nets, and we are seldom disappointed. The cause of the elevation in temperature is thought to be directly connected with the prevailing wind from the southeast, where the Gulf Stream lies

It is believed that the fact that the differences in the temperature of the water — now warmed by the Gulf Stream, now cooled by other currents — is what gives such a great variety to the marine fauna from Cape Cod southward.

regions really are.* It can hardly be supposed that different physical conditions and environment, as far as the coast line itself is concerned, could have brought about such a great difference and such a restriction in these floating pelagic animals. The great influence in their limitation must be the temperature of the water, and its difference in the two localities.

As strictly related to this line of inquiry is a suggestion in regard to the possible medusan fauna of a region contiguous to the Bay of Fundy. It is a well-known fact that the southern part of the Gulf of St. Lawrence, near Prince Edward's Island, presents us an assemblage of southern genera of Mollusca, surrounded by strictly boreal forms. It would be very interesting to discover what the character of the hydroid and medusan life of this warm area is, and to see if we have, as in the case of the Mollusca, a colony of southern genera protected in their northern home by the higher temperature of the water. I have been unable to visit this locality for study, but I commend the problem to those who engage in marine work on this coast. Unfortunately we know next to nothing of the acalephian fauna of this region of the Gulf of St. Lawrence.

CTENOPHORA.

Mertensia ovum, Mörch.

The common tentaculated Ctenophore at Grand Manan resembles *M. ovum*. It is not rare near Eastport, where I found it in the summer of 1885 in considerable numbers. It was taken in some abundance at Grand Menan in 1886.†

* Tabular lists of medusæ from the Bay of Fundy region and from that of Narragansett Bay are given by A. Agassiz in the "North American Acalephæ." The well-marked contrast which one can easily see in these lists appears even more striking when we add to those of the Bay of Fundy some of the characteristic boreal genera here mentioned.

† Ova of a Ctenophore were found in great abundance at Grand Manan in July and August, 1886. These were traced into young Mertensiæ, and are possibly of this species. They look unlike the eggs of Pleurobrachia found at Newport. The fact that *Pleurobrachia rhododactyla*, recorded by other observers from Eastport, was not seen by me does not mean that it is not thought to exist there. I have only spoken of jelly-fishes observed, and do not wish this paper to be regarded as a list of medusæ which live in the Bay of Fundy.

Bolina alata, Ag.

This beautiful specimen of Ctenophores was found once, but there is reason to believe that it is common in the Bay of Fundy.

In the few specimens which were seen there were no parasitic Actinians in the body, as is found in the related Mnemiopsis from Newport. Of course, negative evidence of this kind may not mean much, for early in the season at Newport none of the specimens of Mnemiopsis have specimens of Actinians * in their chymiferous tubes or stomachs.

Beroë roseola (Ag.).

Several specimens were found at Grand Manan.

SIPHONOPHORA.

Nanomia cara, A. Ag.

Plates I., II., III.

The only Physophore which was captured at Grand Manan is the interesting medusa called by A. Agassiz † *Nanomia cara*. This jelly-fish, described many years ago, has been repeatedly mentioned in text-books and general works on zoölogy, but since its discovery nothing has been added from direct observation to our knowledge of its anatomy and somewhat exceptional embryology ‡ as made known by A. Agassiz. It was therefore with much enthusiasm that I first saw from the wharf back of the Dominion House at North Head, Grand Manan, many specimens of this beautiful animal swimming in the water. As is well known, many interesting and doubtful details of anatomy remain yet to be made out in regard to this animal, and it was with keen pleasure that the medusa was captured in abundance and placed in aquaria for study.

* It is, however, an interesting fact that I went directly from Eastport and Grand Manan to Newport, and on my arrival there, not more than five days after leaving the northern localities, plenty of Actinians in Mnemiopsis were found. The yearly record of the time of the appearance of this parasite at Newport shows it much earlier in other years than at the time I was at Eastport.

† Proc. Bost. Soc. Nat. Hist., IX. 181; North American Acalephæ, Illust. Cat. Mus. Comp. Zoöl., II. 200–213; Seaside Studies in Natural History, pp. 76–83.

‡ Although nothing has been added to a knowledge of its anatomy and development, the possibility that a closely allied Physophore occurs in the Arctic is commented upon by Moss and by the author. So little is known of the generic characters of the Physophore supposed to be Nanomia from Robeson's Channel and Lady Franklin Bay, that we cannot definitely say they are the same. There seems no good reason to doubt their identity.

As the only figures which we have of Nanomia are of the young, my first care was to obtain a figure (Plate I.) of the adult animal.

The method by which a drawing of the outline of this large Nanomia was made may have an interest to those engaged in the study of the Siphonophores. The outlines of Plate I. were drawn in the following way.

The animal was placed in an upright glass jar, with flat sides, similar to those of glass vessels used for the bath in photography. This glass receptacle was placed in the bright sunlight, on a table between the observer and the window, or some source of light. It was so placed that a well-defined shadow of it was projected on the paper held a few inches back of the animal, on the side of the glass opposite the window. The paper was tacked to a board held upright and firm by simple means, which any one can devise. The shadow of the Nanomia was so clearly defined that even the faintest lines of outline were seen projected on the paper. There are times when a Siphonophore floating in the water keeps almost perfectly quiet for some minutes. This is a good opportunity to trace on the paper the lines of the shadow with a pencil. Although I could not make the whole contour before a new movement of the medusa, it was easy to draw the nectocalyces and sections of the polyp-stem before the animal changed its attitude.

The only trustworthy account which we have of Nanomia is the original description by A. Agassiz.* This observer not only described the first long-stemmed Physophore from American waters, but he also gave the first series of recorded observations on the development of the young of any genus of Siphonophores.

From my own studies of Nanomia I am convinced that the adult of Nanomia has never been figured or described. The reasons for this belief will, I hope, appear as I go on in my account. The description by A. Agassiz was pioneer work in a field where later observations have been extensively made; yet for over fifteen years Nanomia was the only long-stemmed Physophore known from the waters of the United States. His description has been repeatedly copied, and his figure is widely used in general accounts of these animals. It is found necessary to differ from one or two statements made in the original description in regard to Nanomia. These differences are specially noted, and a redescription is not made of those points of anatomy where in the main my account agrees with that already published. The fact that Nanomia more than any other Siphonophore is used in text-books and general descriptions of marine animals published in America to illustrate the general character of the group, would seem an inducement to publish any contributions which might be made in regard to its embryology and anatomy.

It may be well, at the very threshold of my description, to mention the

* The best account of the anatomy and embryology of Nanomia is in "North American Acalephæ." There are other notices of the same animal by the same author, one of the best known of which is in "Seaside Studies," by Mrs. E. C. and A. Agassiz.

reasons which led me to regard the published figures of the adult as the young, and not the adult Nanomia.* One of the most important reasons which have influenced me is the small size and the small number of nectocalyces. While the specimen figured is barely six inches long, specimens of Nanomia were often found at Grand Manan four and five feet in length. While A. Agassiz never found more than four pairs of fully developed nectocalyces, many of the adults had fifteen pairs of these structures.

A more important fact, however, which would seem to indicate that the figure is that of a young animal, is the following. The great number of embryonic tentacular knobs,† or those described on the "first set of polyps," show immaturity; for these knobs are always confined to young or larval forms in related genera, like Agalma, Halistemma, and Stephanomia. The adult permanent knobs, or "corkscrew-shaped tentacles," are all immature. The adult form of these knobs is not attained in any of those of Nanomia yet figured.

In order to facilitate the reader in a comparison of my description with that in the "North American Acalephæ," the following table is introduced. The terms in the first column are from the published account, those in the second are made use of in the present description .

First set of polyps	Embryonic polypite with embryonic tentacular knobs.
Second kind of polyps	Undeveloped permanent polypites with undeveloped permanent knobs.
Third kind of polyps	Hydrocyst, taster.
Fourth kind of appendage (p. 206)	Undeveloped hydrocyst, taster.

The largest specimen captured measured, when extended, over four feet; when retracted, its length was three feet. The specimen which is figured, of life size (Plate I.), was one of the most convenient for study, but not one of the largest. It may safely be said that hundreds of specimens of the size represented were taken just off the wharf near the Dominion House at North Head, Grand Manan.

The adult animals, as they float extended in the water, can readily be distinguished by a practised eye from the southern Physophore, *Agalma elegans*. The whole external appearance of the two genera is different. The tentacles of Nanomia are carried in a different way from those of Agalma, and are not drawn to the polypites in the same clumps, while the tentacle itself is more often thrown into festoon-like folds, as shown in the figure. It is needless

* North American Acalephæ, Illust. Cat. Mus. Comp. Zoöl., No. 2, p. 201, Fig. 332.

† On many of the small specimens of Nanomia from Grand Manan, embryonic knobs (Plate II. Fig. 8) were found. These closely resemble the knobs figured by A. Agassiz. They were not found in adults as far as observed.

to say that Nanomia is no less graceful than the beautiful "sea necklace," Agalma, in all the motions of tentacles and tentacular knobs.

Axis. — The axis of Nanomia is long, highly flexible, muscular, dotted with reddish pigment spots. It is divided into two regions, which may be known as the nectostem (*ns*) and the polyp-stem (*ps*). The length of the latter is several times that of the former. The polyp-stem appears to be more easily bent than the nectostem, but this appearance is brought about by the rigidity imparted to the latter by the close approximation and form of the nectocalyces. It is needless to say that the axis, as in all Physophores, is hollow throughout, and that from it most of the appendages of the colony have arisen.

Float. — The float (*f*) resembles that of other Physophores. It is a small sac enclosed in an enlargement of the axis, and has reddish pigment in its outer walls. The contents seem to be a bubble of air or gas, as in other Siphonophores. The longer axis of the float does not coincide with that of the axis of the Nanomia, but is bent at a small angle.

Nectocalyces. — The nectocalyces (*nc*) are biserial in their arrangement, with bell openings pointing in opposite directions. Their close approximation imparts to the stem (nectostem) a rigid character, which however disappears when their connection with it is once broken. The rows of nectocalyces are transparent, gelatinous, almost invisible as the animal swims in the water. Near the float there is a small cluster of undeveloped bells, the full grown being more distant from the float than the less developed. The specimen figured has thirteen pairs of well developed nectocalyces. Each nectocalyx is bell-shaped, fastened to the axis at the apex, and has two lateral horns or spurs, shown in the figure in profile, which interlock with corresponding spurs from the opposite side of the axis.

The structure of the bell and its tubes is well described by A. Agassiz. The bell is rounded, with small circular orifice, slightly closed by a thin velum. The bell cavity is spacious. The chymiferous tubes are four in number, in addition to a marginal vessel and a single tube communicating, through the point of union of the bell and stem, with the cavity of the axis of the animal.

The fact that the nectocalyx is slightly flattened on the upper and lower sides, and the existence of a corresponding bulge on the remaining sides has brought it about that, while the radial tubes of the nectocalyx of the former spheromeres is regular and straight, passing from common junction directly to bell rim, those of the two lateral spheromeres are tortuous, forming a single loop, as shown in the figure (Plate III. Fig. 2). This character is by no means peculiar to Nanomia, but is an interesting fact in the asymmetrical development of the bell.

Hydrophyllia. — The bracts, covering scales, or hydrophyllia (*hph*) are colorless, transparent bodies, covering the bases of the appendages to the polyp-stem. Each hydrophyllium is irregularly rectangular to triangular in shape. Two adjacent sides of the rectangle are so elongated that a triangular

shape is given to these bodies. The free and distal angle diagonally opposite the angle of attachment is rounded and very obtuse ; the angle of attachment is more acute.

A tube extends from the point of attachment diagonally to the opposite angle of the covering scale, where it ends blindly. This tube is undivided, unbranched, with entire edges.

Polypites. — The polypites (*p*) are flask-shaped bodies, attached by a short peduncle to the polyp-stem. Their free end is open, forming a mouth. The rim of this orifice, or the lips, are without appendages. The basal peduncle is short, and of somewhat smaller diameter than the polypite itself. Near the base the polypite bears a "Wimperwülst," or ferule-like thickening of the walls.* At that point reddish pigment is found, and buds which are immature tentacular knobs arise. The tentacles also originate at that point. The polypites are regularly distributed along the polyp-stem, dividing the stem into sections or regions, which may be known as inter-polyp regions. The oral extremity of the polypite, except when it is retracted, extends beyond the hydrophyllia. The opening of the mouth sometimes expands, by which the lips become trumpet-shaped. The rim of the mouth is entire. Fragments of food were seen inside the polypite. Rows of large cellular bodies, in parallel lines, extend along the inner wall of the polypite. These are possibly hepatic in function.

Tentacles. — The tentacles (*ta*) are long, filamentous bodies, arising from the base of the polypite. They are highly contractile, and generally, when the animal is at rest, extended. Each polypite has a single tentacle. There are two kinds of tentacles, one of which bears tentacular knobs, the other being destitute of the same.† The former, which are the tentacles proper, are those which arise from the polypites ; the latter, the filaments of the hydrocyst, which have no tentacular appendages.

The peculiar festoon-like way in which the tentacles are often carried, is noticed by A. Agassiz. This habit is marked in the genus, and is more common in Nanomia than in the southern genus Agalma. Although I have studied all the Mediterranean species of Physophores alive, I recall none where this habit is so well marked as in Nanomia.

Tentacular Knobs. — The adult tentacular knobs (Plate II. Fig. 9) of Nanomia resemble those of Agalmopsis, Fewkes.‡ The various parts which enter

* This increase in size of the polypite at the "Wimperwülst" is largely owing to the increased development of the middle layer of the body.

† The tentacles which are destitute of tentacular knobs do not arise from polypites, but from the hydrocysts.

In the growth of the tentacles the tentacles do not first form, and then the tentacular knobs bud from it, but the knobs first form on the "Wimperwülst," and then the tentacle is pushed out, bearing these bodies, already imperfectly formed.

‡ One form of Agalmopsis, Sars, *Stephanomia pictum*, Metsch., *Halistemma tergestinum*, Claus, *Agalmopsis fragile*, Fewkes. These various aliases of Agalmopsis are mentioned, lest confusion be introduced by the above statement.

into the formation of the tentacular knob are the peduncle, the involucrum, the sacculus, and the terminal filament.

The terminal filament (*ft*) is long, thread-like, single, arising from the distal end of the sacculus. In its walls are imbedded many lasso-cells, or nematocysts. The sacculus is closely coiled in several turns. It is a large reddish body, armed with batteries of lasso-cells, and crossed by prominent lines.

The involucrum (*inv*) forms a cap over the sacculus.* It is bell-shaped, with entire edges, the sacculus (*sac*) arising from the inner central point. The whole tentacular knot hangs from the tentacle by the peduncle.

Tasters.†—Among the most interesting and it would seem exceptional structures in the genus Nanomia are those organs which are known as tasters (*ht*). The most marked peculiarity in their anatomy is the existence of an "oil globule" (*og*) near their base.

The tasters hang from the polyp-stem midway between the polypites. A single adult and many half-developed tasters occur between each pair of polypites. Individual tasters are small, slender, flask-shaped bodies, resembling immature polypites. They arise directly from the stem and are destitute of a basal peduncle. The distal extremity is closed.

Each taster bears near its attachment a prominent red body of spherical shape, known as the "oil globule." The taster has a single long tentacle (*h ta*), destitute of lateral appendages. In the water in which Nanomia was kept alive, several tasters which had separated from the main stem were found floating about near the surface. These were not seen to grow into colonies of Nanomiæ, but gradually became opaque and decayed, never in those studied growing into new colonies.

Gonophores.—A. Agassiz supposed that separate male or female colonies of Nanomia were found. He considered that some colonies of this genus are all males, while others are all females. My observations differ in this respect from his. The adult Nanomia, like the genus Agalma, has male and female bells on one and the same colony.

The sexual bells (*g*) of Nanomia are found near the base of the tasters, where they form botryoidal clusters. These clusters occur on all parts of the polyp-stem wherever hydrocysts are found. The interior of the male bells in many cases has a milk-white color, while the female bells are always transparent. Each male gonophore is bell-shaped and fastened to the base of the cluster by a short flexible peduncle. The walls of the bell are thin, with four radial tubes joined to a marginal canal. The peduncle is penetrated by a

* The name sacculus has been given to the coiled red structure which forms the larger part of the knob by others. It seems more natural simply to interchange the terms, so that what is now called the involucum may be known as the sacculus, and *vice versa*.

† The term "taster," used to designate these structures, is open to some objections, but is regarded as one of the best which has been suggested to apply to these peculiar organs in the Physophores.

vessel which connects this radial system of tubes with the cavity of the axis of the colony. The bell margin has a marked velum and is destitute of tentacles. The sperm is found in the inflated proboscis, which fills almost the whole bell-cavity. This receptacle is in older male bells, and in those especially which are found near the extremity of the polyp-stem, of a milk-white color. The spermatozoa have a rounded head and small vibratile tail. The clusters of female bells which occur with the male have a similar attachment, and are also campanulate, resembling those of Agalma. Each bell carries a single ovum. Individual eggs and bells voluntarily separate from the attachment to the colony, and the latter live for some time free in the water. The ova of Nanomia can easily be seen by the unaided eye, as they float about in the water in which a parent Nanomia is captive.

A method of collecting the ova is to allow the Nanomia to remain quiet for some time in a glass jar. This jar contained about three gallons of water, and was so placed on a table that one could see through its sides, the window or source of light being on the opposite side of the jar. In this way the ova could readily be distinguished in the water, and after a few hours they rise to the surface. When they are seen floating at different depths in the water, it is possible to pick them out one by one with a pipette. When the ova rise to the surface it is more convenient to skim them off by means of a watch-crystal, or some similar shallow receptacle.

Development. — The development of the older larvæ of Nanomia, after the formation of the float, has been well described by A. Agassiz in his account of the animal, to which reference has already been made. He considers that there are two methods of development, one from the egg, and the other by budding from the parent colony His figures are mostly from stages which he regards as formed by the latter method, and are of larvæ after the float has already formed.

It is certainly an exceptional method of growth of new colonies of Siphonophores to find the young budding from the parent, and new observations are desirable to determine the details of such growth. There is no known genus which resembles Nanomia in this respect, and all other genera, whose embryology is at present known, reproduce new colonies by ovulation alone. The following observations have a bearing on the origin of the larva of Nanomia, although they leave the important question in doubt.

A minute comparison of the float of the parent colony with the "oil globule" of one of the tasters was made, in order to detect differences and resemblances, if any, between them. While it was found that there are marked differences in these two structures, I could not say that the differences would prevent the one being a development of the other. Still, I have not been able to persuade myself that such is the case. I have repeatedly found the tasters with their oil globules detached from the parent axis, but all attempts to raise these into older stages similar to those figured by A. Agassiz have failed. There is one point in which there is a great difference in the tasters which I

have studied and the youngest larva he figures. They differ from the stages which he figures in the presence of the tentacle which always characterizes the taster. A failure to raise one of these tasters separated from the colony into a new colony, it might be said, does not prove that under other conditions better results may have been reached. As a question of opinion, it is regarded as highly doubtful that the colony of Nanomia reproduces by budding, and that the new colony is ever formed from a taster. Nanomia, however, as shown by Agassiz, has an egg development, and passes directly from a planula-like young into stages similar to the youngest which he figures. It is therefore thought that the embryo, without exception, is derived from an egg. The segmentation of the egg was observed, and, as nothing has ever been published on the egg of Nanomia, a few stages in the segmentation are here represented.

The egg of Nanomia, like that of Agalma and other genera, is transparent, colorless, almost invisible in the water. The interior is penetrated by and almost wholly made up of a spongy mass of protoplasm, forming a network filling the contents of the egg. A thin covering of protoplasm surrounds the egg. Metschnikoff * describes in the egg of Epibulia a similar network, and the author † has devoted some space to a consideration of the same in Agalma.

The first change (Plate II. Figs. 1, 2) in the external contour of the Nanomia egg is the formation of a primary cleavage-furrow. This furrow was formed by the bending in of the outer wall of the egg at one pole. This infolding of the primary furrow leads to well-marked folds on the outer wall of the egg, which recall the phenomenon of "Faltenkranz" in some other animals. In about an hour's time after the first appearance of the infolding to form the primary furrow, a 2-celled cleavage stage was formed, and the first cleavage plane (1 *cl*) is well developed. About another hour elapses before the second cleavage plane is formed and a well marked 4-cell stage (Figs. 4, 5) is developed.

In his paper on the development of Agalma the author points out the peculiar warping of the first cleavage plane by the formation of the second. It was there shown, that by the growth of the second cleavage furrow at right angles to the first, it was brought about that the plane of the first cleavage was broken near the equator of the egg. In the same way and by an analogous process in the development of the Nanomia egg the second cleavage plane is so formed that the continuity of the first plane is likewise broken. Figure 4 of Plate II. illustrates this broken condition of the plane in Nanomia. Whether this modification is of any morphological importance, or has any influence in subsequent development of the cells, cannot be at present determined. The 8-cell stage is produced by the formation of two new furrows (Fig. 6) bending in on one side of those cells already formed in a way analogous to that already described in Agalma.

* Studien über die Entwickelung der Medusen und Siphonophoren. Zeit. f. Wiss. Zoöl., Bd. XXIV.

† On the Development of Agalma, Bull. Mus. Comp. Zoöl., Vol. XI. No. 11.

The egg of Nanomia in the eight-cell stage is the oldest which has been studied. There seems to be nothing peculiar in the method of segmentation as compared with that of Agalma. Among other medusæ it has some likenesses with that of the Ctenophora and certain Trachymedusæ.

Between the eight-cell stage and the youngest as figured by A. Agassiz there is a considerable gap, which I am not able to fill by new observations. This interval is, however, in part bridged by observations on an allied genus found in the Mediterranean, already published by Metschnikoff. This observer * has studied a Siphonophore, which is closely allied to Nanomia, and seems to resemble in mode of growth, as far as known, that which has been already described and figured by A. Agassiz.

Older larvæ, which he supposes to belong to the same genus, Metschnikoff has raised from planulæ which are a little younger than the youngest Nanomia figured by A. Agassiz. He has shown that in these larvæ no "primitive hydrophyllium" † is formed, and that the first structure to develop is the float. He regards his genus as the same as Nanomia.

A few years ago I was inclined to regard the genus referred to by Metschnikoff as the same as Nanomia. The adult tentacular knobs described for the first time in this paper confirm me in that opinion, but there is one thing which leads me to doubt their identity. The existence of the large oil globules in the bases of the tasters is very exceptional among Physophores. I have studied the animal, *Stephanomia pictum*, referred to by Metschnikoff, and was one of the first to describe it,‡ but I do not remember seeing structures similar to the "oil globules" of the tasters of Nanomia. In the published descriptions of this animal there are no similar structures. The question then arises whether the presence of this structure is sufficient to sep-

* *Op. cit.*

† The term "primitive hydrophyllium" was suggested in my paper on the development of Agalma to designate the cap-shaped covering scale which forms such an important organ in determining the form of the larva. The designation "primitive larva," used to distinguish the stage in which this organ is most developed, was suggested in the same paper. The primitive larva is supposed to be an ancestral form of Calycophores and Physophores, and to be closely allied to the ancestral form of other Hydromedusæ.

‡ Contributions to a Knowledge of the Tubular Jelly-fishes, Bull. Mus. Comp. Zoöl., Vol. VI. No. 7, pp. 136, 137, Plate II. Neither in Metschnikoff's figure of Stephanomia, nor in Claus's figure of *Halistemma tergestinum*, which all seem to regard the same, the relative size of the hydrophyllia seems to be smaller than in Nanomia. The same is true of my Agalmopsis from Florida. Claus's figure of the taster of his Halistemma, Plate II. Fig. 4, shows what may be a small "oil globule" near the base of this organ, and the structure in the same figure lettered *m g*, "male sexual bell," has some resemblance to the "oil globule" of Nanomia. Still from his description it does not seem that the "oil globule" has the predominance in size which it has in Nanomia. It must also be said that if *m g* (Plate II. Fig. 4) is a male sexual bell, it is very different from the same bodies in Nanomia.

arate Nanomia from the allied Stephanomia, auct., Halistemma, Claus, and Agalmopsis, Fewkes. We have on the Florida coast an Agalmopsis, *A. fragile*, Fewkes, which has the same knot as Nanomia, and in other particulars is very near it. They are not the same species, although generically they seem to be very close. For the present I adopt Agassiz's name, Nanomia, not because it differs from other Siphonophores in the way some have thought, but on new grounds, or because of the marked character of the "oil globule" in the taster of Nanomia. In all other respects Nanomia is like Agalmopsis, Fewkes, from the Mediterranean and Floridan Seas.

It is predicted that the egg of Nanomia will be found to develop at first a float, and then an embryonic tentacle with embryonic knobs; that there is never developed a primitive hydrophyllium; and that an Athorybia-like covering scale does not form. The type of development, as compared with that of Agalma, is more abbreviated, and consequently more direct in Agalmopsis than in Nanomia.

The facts which lead to this conclusion may be seen from what is said below. The state of our present knowledge of the development or growth of the larval stages of Nanomia may be shown in the following historical summary: —

1. The larva in which the float is fully formed is traced from older larvæ into the genus Nanomia. This series of observations was made by A. Agassiz, the discoverer of Nanomia, who considers that the youngest stage (with float only) develops from a bud, and also from the egg. The earliest stage which he figures he regards as identical, whether formed by either method of development.

2. Metschnikoff obtained younger stages, or those before the float is developed, of an allied Physophore. The youngest stage which he figures is a planula.

3. The author here describes the segmentation of the egg of Nanomia into the eight-cell stage.

The only break now in a consecutive series of observations is between two and three, or the eight-cell stage and the planula. Judging from what we know of other Siphonophores, no embryonic structures appear in this gap, and we are justified in supposing that no primitive hydrophyllium, or covering scale, appears before the float in Nanomia.

The fact that in Nanomia no primitive hydrophyllium, such as is found in Agalma, exists, does not prevent our recognizing in the youngest larva with a float, and a tentacle with embryonic knobs, all the parts of the stage called the primitive larva. Metschnikoff has shown that a Siphonophore float is homologous to a bell,* and I have no hesitation in accepting the theory that the float of Physophores is homologous with one of the nectocalyces of the

* The primitive larva, or, as I have elsewhere called it, the primitive medusa, from which all the Siphonophores have phylogenetically arisen, would seem to be somewhat like older stages on Plate III. of my "Development of Agalma," Bull. Mus. Comp. Zöol., Vol. XI. No. 11.

Calycophores. In 1883 the float was compared with the anterior nectocalyx of Diphyes. I regard the first nectocalyx of Monophyes as the same as the primitive hydrophyllium of Agalma.*

In the phylogeny of the Siphonophores, both Physophores and Calycophores have a stage called the primitive larva in common, and it is possible their ancestor was not unlike the so-called primitive larva stage of Agalma, with a single cap-shaped hydrophyllium, one polypite, and a knob similar to that which I have called the embryonic knob (Plate II. Fig. 8). The Calycophores retain certain organs which characterize this form, as the primitive hydrophyllium and the embryonic tentacular knob. In the Physophores, however, a specialized float, a modified bell, is developed, the embryonic knob gives place to other kinds of knobs, characteristic of the different genera of Physophores.

The primitive larva preserves the Medusa form, and may be supposed to approach more closely the ancestral form of the Siphonophores among other Hydromedusæ than any other medusiform larva. The name primitive larva appears to me to be a good one, and can well be accepted as a help in studies of the phylogeny of the Siphonophores.

I have already elsewhere devoted some space to showing that the primitive larva finds its nearest homologue among Hydromedusæ, in certain Tubularian medusiform gonophores. I chose Lizzia for my comparisons. It was perhaps premature for me to take any one genus for such a comparison, and it might have been better to have chosen the Trachymedusæ instead of the Tubularians for such an homology. From the character of the egg cleavage, and the fact that the development, as far as known, is similar in the Siphonophores and genera of Trachymedusæ, it is possible that the young stage of the former, which I have named the primitive larva, is more closely related to certain medusiform larvæ among the Trachymedusæ than to genera like Lizzia. The close homology between a medusiform gonophore and a simple hydroid, however, is such that I think we are justified in regarding the young of Nanomia with a float and no primitive hydrophyllium as homologous with the primitive larva of Agalma. I believe the ancestral form of all Hydromedusæ, as well as of all the Siphonophora, will be found to be similar to the primitive larva of Agalma in its younger stages. It had the form of a ciliated planula, with an enlargement at one end and a mouth at the opposite. The enlargement at one end was formed of three layers, is bell-shaped or gelatinous, and forms the bell of the Medusa, the float of Nanomia, and the primitive hydrophyllium of Agalma. In the fixed hydroid it becomes a base of attachment, in Rhizophysa or Nanomia a float, and in Agalma a covering scale. It is well to have some name to designate this prototype, and no one has suggested any better one than the "primitive medusa." †

* Embryological Monographs, No. III. Plate VII., Mem. Mus. Comp. Zöol., Vol. IX. No. 3.

† It would be interesting to trace the resemblance of this primitive larva or

HYDROIDA.

Sarsia mirabilis, Ag.

Many specimens of Sarsia were seen at Grand Manan on a single excursion. Later they disappeared, and were not again collected. The hydroid Coryne * was also found.

Hydrichthys mirus, gen. et sp. nov.

Plates IV., V.

During the month of August of the past summer (1887), in the surface fishing carried on at the Newport Marine Laboratory, I captured a most interesting genus of parasitic hydroid. This genus and its peculiar life are undescribed as far as known. The mode of parasitic life is most extraordinary, and the modification of its structure of an anomalous character.

A small fish of the genus Seriola (*S. zonata*, Cuv.) was taken in the dip-net at a time when the sea was quiet.† Upon the side of the body (Plate IV.

primitive medusa, the ancestral form of the medusæ, with the prototype ("Pilidium-like larva") of the six groups of marine larvæ described by Balfour. It is thought that such a resemblance not only exists, but also has an important phylogenetic meaning. It is not in place to discuss this question in this paper.

It may be asked whether the primitive larva of Agalma, with its huge primitive covering scale, or the primitive larva of Nanomia, where that scale is replaced by a float, is nearest the primary or ancestral larva of Hydromedusæ. The youngest forms of the primitive covering scale and the float closely resemble each other, and the departure from that form seems greater in Agalma than in Nanomia. A nectocalyx seems more highly organized than a pneumatophore; still, between a primitive hydrophyllium, such as exists in Agalma, and a float like that of Nanomia, it is hard to tell which is more highly specialized. It cannot be said that the adult Nanomia is less highly specialized than the adult Agalma. Although the float of Nanomia is first formed, it follows the primitive hydrophyllium in Agalma. While this fact might seem to indicate want of homology of the float in the adults of the two genera, it does not seem to prevent our considering the primitive larva to be represented by the young Nanomia with a float and no covering scale.

* Although it was not my intention to speak of the hydroids collected in the Bay of Fundy, I must mention beautiful specimens of Corymorpha dredged in shallow water not far from Eastport. The medusæ were just ready to drop from the hydroids, and as they were almost mature in July probably in later months they are found in abundance free swimming in the sea. I was of course on the look-out for the so-called free hydroid Acaulis, Stimpson, and other similar hydroids, but was unable to collect any of these animals. The broken heads of the hydroid Pennaria, which somewhat resemble Acaulis, were found.

† The Seriola was in company with two others. Neither of its companions, however, were afflicted with the parasites mentioned below.

Fig. 1) and near the anal opening of this fish a patch of reddish-colored bodies was noticed. This patch was at first supposed to be a fungoid growth from a wound or abrasion of the body. A more careful examination of the supposed fungus showed me my error, and revealed the fact that it was an attached animal with true hydroid affinities. The fish with the attached hydroid was kept alive in an aquarium for some time, and from the hydroid many medusæ (Plate V. Figs. 1–3) of interesting relationship developed. Thousands of these medusæ were raised, and the general characters of their structure and external anatomy studied. They seem to be hardy in their younger stages, but it is doubtful whether I have raised them into adults.* The form of the medusa is quite different from that of any known genus thus far found at Newport, but not unlike in general affinities certain well-known tubularian genera commonly found there in surface fishing.†

The exceptional, and it is believed unique, condition in Hydrichthys is the character of the hydroid, and the unusual feature its attachment to the sides of the body of the fish as a parasite or commensalist.‡ The polymorphic structure of the hydroid is quite different from that of any known hydrozoön.

The modifications in the anatomy of the hydroid are believed to have been in part due to its attachment to its host. This supposition, if it is well founded, and the additional fact that Hydrichthys has never been found in any other habitat or attached anywhere else than to the body of an osseous fish, may mean that we have in this genus a case of parasitism, or possibly commensalism, and that this condition has rendered functionally useless or modified the form of certain structures commonly present in other hydroids, while it has increased in relative size and possibly importance other organs, especially those concerned in reproduction and the dissemination of the young. Hydrichthys, looked at in this light, presents us with one of the most interesting conditions of hydroid life which has yet been recorded.

It was impossible to determine how much nourishment the hydroid Hydrichthys draws from the fish upon which it lives through the network of tubes from which the gonosomes and filiform bodies arise. The absence of tentacles, or organs the function of which is the capture of food, would seem to deprive Hydrichthys of those means of capturing and drawing food to the mouth which are almost universal among fixed hydroids. Possibly in its parasitic life the hydroid obtains its sustenance from the fish on the sides of which it lives.

The question whether the fish ultimately succumbs to the parasite is an interesting one, but one which cannot be definitely answered at present. The only specimen of Seriola captured which was infested by the hydroid appeared to be well and healthy, and lived for a considerable time without exhibiting

* The oldest medusa raised from the parasitic Hydrichthys has four tentacles.

† *Sarsia mirabilis* and *Ectopleura ochracea*.

‡ From my limited knowledge of Hydrichthys we are not justified in considering it a commensalist.

any inconvenience from the attached parasite. The muscles of the fish, however, under the "basal plate" of the hydroid were somewhat wasted; and after the fish was killed, the shrinkage in its body walls seemed to indicate that the fish had not wholly enjoyed his strange companion.

Hydroid. — The hydroid colony of Hydrichthys forms a cluster of reddish and orange-colored bodies attached to the sides and circumanal region of *Seriola zonata*.

The base of the whole colony is about three fourths of an inch in lateral extent. The base of attachment to the fish is a flat thin plate with ramifying tubes, by means of which the colony is fastened to the fish, and upon it separate clusters of sexual bodies (gonosomes) and filiform structures (hydranths?) are united together. The structure of the flat plate is not peculiar to Hydrichthys, but resembles that of many other hydroids attached to submarine objects, as Perigonimus and Hydractinia. The walls of the basal plate are leathery, or coreaceous, rather than calcareous. This basal plate is destitute of prominent projections such as exist in Hydractinia, but is smooth both above and below.*

In studying the character of the basal plate of Hydrichthys I was reminded of the anastomosing tubes on the under side of the float of Velella.

Each gonosome (Plate IV. Fig. 2) is botryoidal, consisting of an axis and lateral branches with medusæ in all stages of growth. The axis of the gonosome arises by a single trunk from the basal plate, and tapers uniformly from attachment to apex, opening† at the free end into the surrounding water. This axis resembles in its histological structure the stalk which bears the medusiform gonophores or Chrysomitræ in the genus Velella. It is sensitive, highly contractile when touched, transparent, or but slightly colored.

The side branches are similar in structure to the stem. They are generally simple, but sometimes subdivided or branched. The lateral branches near the base of attachment are longer than those near the free end of the stem. The side branches are of uniform diameter, and arise irregularly from the main stem. Like the main stalk, they have a cavity within, which communicates freely with that of the main stem.

In specimens preserved in alcohol the lateral branches are short and contracted, but in live specimens both the main stalk and its lateral branches are long and extended. There is no chitinous sheath about the axis or branches. Each lateral branch or supplementary division bears at its free extremity, which is closed, a cluster of medusa buds in all stages of growth from a simple spherical enlargement or expansion of the axis to a medusiform body with two

* The attachment of the basal plate to the wall of the fish is so firm that it is with difficulty broken away. I was obliged to cut it off, and with the hydroid thus dissected portions of the body of the host were also ruptured.

† There appears to be an opening at the free end of the gonosome. I could not determine to my satisfaction that the supposed opening really exists. I could not observe that it was functional.

stumpy tentacles at its free extremity. Small lateral branches without medusa buds are not rare, especially near the free extremity of the main stem. They are small, however, and project but little from the main stem.

The free extremity of the gonosome, or of the main stem of the same, is destitute of medusa buds, and, as has been said above, is without appendage. There are no tentacles about this terminal opening, and its rim is entire.

Whether the terminal opening of the main stem serves as a mouth or not it is impossible for me to say. No food was found in the cavity of the stem, and it is supposed that the whole structure is dependent upon the tubes of the basal plate for its nutrition. The main stalk is not supposed to take in food from the surrounding water through the terminal orifice.

The cluster of buds at the extremity of the lateral branches of the gonosome are the structures which give the color to the colony. They resemble the medusiform buds found in other Tubularian hydroids in their mode of attachment, their general structure, and their mode of growth.

In addition to the botryoidal clusters of gonosomes there also arise from the basal plate by which the colony is fastened to the fish long flask-shaped bodies, recalling in their external form the tasters of the Siphonophores. These bodies (Plate IV. Figs. 3, 5), like the gonosomes, arise from the upper walls of the basal plate of tubes attached to the body of the fish. Like the gonosomes they are numerous in the hydroid colony. The filiform bodies are elongated flask-shaped structures, of about uniform size throughout, arising from different points of attachment at the base from the gonosomes. They are, like the gonosomes, destitute of appendages, but they probably have an opening at the free extremity. The walls of the filiform bodies are composed of an outer thin and an inner thickened layer. There is a cavity within. The walls are dotted with pigment spots, which are especially numerous around the free extremity. In one of these filiform bodies there is a spherical mass, which resembles half-digested food. It is doubtful whether this mass is food. The free end of the filiform bodies is sometimes trumpet-shaped, but ordinarily rounded, the opening being concealed by the contraction of the lips. The bodies of the filiform structures move backwards and forwards on their attachments, and are sometimes spirally coiled in a single turn. They recall in general appearance the spiral zoöids of Hydractinia and the tasters of Siphonophora, but, unlike either of these structures, have an orifice at their free end. They are thought to have close likenesses to the "central polyp" of Velella.

Medusa. — At the extremity of each lateral branch or its subordinate division there is found a small cluster of buds, which is composed of medusæ in all stages of growth. While attached to the branch, and before separation from it, these bodies take on all conditions of growth, from a simple hernia-like spherical bulb to a cylindrical body with two stumpy tentacles. No more than two tentacles are developed in the oldest attached medusa gonophore which was studied. The course of the growth of the medusa of Hydrichthys from a hernia-like bud to a small medusa is in no respect

peculiar, but follows the laws of growth so often described in these structures in related genera.

The cluster of medusa buds is confined to the terminal end of the lateral branches. Near the base of attachment of each bud there is a patch of red pigment. As the medusa grows in size and the proboscis begins to be formed, the shape of the bud gets elongated, cylindrical, and at the same time two opposite tentacles push out on its free margin. The proboscis has a yellow and orange color. The reddish patches of pigment near the base of attachment of the immature bell persist even after the medusa has detached itself from its connection with the lateral branches.

The different layers of the body of the medusa bell (Plate IV. Fig. 4) can be readily seen through its transparent walls. Of these the epiblast, hypoblast, and intermediate layer can be easily recognized. The origin and growth of the radial tubes, and the subsequent formation of the circular or marginal canal, was traced. This growth does not differ from what has already been described in Syncoryne (Sarsia) and several other genera.

The fish (Seriola) was kept alive in an aquarium for several days, and from the attached hydroid many free medusiform gonophores were raised. On the morning following the day when the fish was captured, many medusæ were found in the aquaria, and every day after its capture many specimens ripened from the undeveloped buds, and one by one detached themselves from their union with the gonosome. There is no possibility of a doubt that the free medusa, as here described, has detached itself from the gonosome attached to the body of the fish.

The free medusa (Plate V. Fig. 1), when it breaks its connection with the gonosome, has two short tentacles situated opposite each other on the bell margin. The medusa bell long before detachment had begun the peculiar expansion and contraction which precede separation, and when once free moves gaily about in the surrounding water. Shortly after its detachment, the medusa with two tentacles resembles a young Stomatoca.* The structure of the Hydrichthys medusa just escaped from its attachment to the gonosome is as follows.

The bell is oval, without apical projection, and recalls in outline that of Sarsia. The outer surface is dotted with numerous nematocysts.† Bell walls colorless and transparent. There are four broad radial vessels and a marginal tube. The tentacular bulbs are reddish, without ocellus. Two tentacles arise from tentacular bulbs diametrically opposite on the bell margin. No otocysts on the bell margin. The proboscis is cylindrical, of an orange and yellow color. There are patches of red pigment near its attachment. The mouth is simple, with entire margin destitute of appendages.

* The fact that Stomatoca is a medusa of Perigonimus was pointed out by Haeckel, Allman, Hincks, and others.

† These nematocysts are most prominent in younger stages in the growth of the medusa. They are well marked even before the medusa form is attained.

The medusa with two opposite tentacles was raised into one with four (Plate V. Fig. 2), passing out of the stage resembling Stomatoca into one like Sarsia.

The form of the bell and the arrangement of tubes is unchanged in the passage from the medusa with two tentacles into one with four. The new tentacles form on the bell margin, half-way between those already formed. They arise near the junction of the radial and marginal canals. All the tentacles now grow to a great length, and the medusa, once very active, sinks to the bottom of the aquarium. Its motion is from now on more sluggish than before, either from exhaustion or habit. I was unable to raise them into medusæ with more than four tentacles.

The affinities of Hydrichthys would not be difficult to make out if we were to deal with the medusa alone. So close are the resemblances with such genera as Sarsia, Ectopleura, and other allied Tubularians, that there would have been no doubt in my mind, if I had the medusa alone to deal with, that Hydrichthys is a close ally of these genera. It is the form of the hydroid which complicates the problem in regard to the affinities of the parasite, for, so far as the hydroids of the Tubularians allied to Sarsia are concerned, there are none which have any resemblance to the hydroid of Hydrichthys.

If we approach the study of Hydrichthys from the hydroid side, remembering the undoubted affinities of the medusa, it seems to me that we must regard the modifications in its structure and its polymorphism as due to the attachment to the walls of its host, the fish. We know, of course, too little of the other possible habitats of this strange hydroid to declare that it is never found in any other place, but the general structure of its body would seem to point to a special modification of its structure brought about by its parasitic life.

The peculiarities of structure which separate Hydrichthys from other allied Tubularian hydroids are the total absence of tentacles, combined with a polymorphism in which there are two kinds of individuals already described, viz. botryoidal gonosomes and filiform hydranths (?).*

In all Tubularian hydroids there are tentacles of some kind or other near a mouth opening. In Tubularia, for instance, we have circles of tentacles arranged about a mouth, and from the intertentacular regions or intervals on the head hang down grape-like clusters of gonophores. Suppose, for purposes of comparison with Hydrichthys, that in Tubularia the chitinous sheath of the single hydroid is absent, the tentacles reduced to nothing or absent, and the

* It might be supposed that the second of these are simply the main stem of the gonosomes, stripped of lateral branches with medusa buds. The differences in the structure of the two show the error of such a supposition. It might be objected to my interpretation that there are two kinds of individuals in Hydrichthys, on the ground that the filiform bodies are undeveloped gonosomes. That objection is also believed to be poorly supported, for young gonosomes differ even as markedly as the adults from the filiform bodies. The designation of the filiform bodies as hydranths is simply conjectural.

whole head modified into the form of an elongated axis or stem. By these changes the clusters of grape-like organs would appear as lateral branches of a main stem ; and if we suppose the clusters of gonophores pushed out to their tips, we should have an exact resemblance to the condition of the gonosomes * of Hydrichthys, where they are simply botryoidal clusters of immature medusæ mounted on peduncles which arise from a common stalk. How is it with the filiform bodies of Hydrichthys ? In reply, it may be said these do not occur in Tubularia. Morphologically, they may be supposed to be the single simple hydroid, stripped of tentacles, gonophores, and enveloping sheath, so that the axis alone, with its terminal opening, is about all that remains. By this reduction we have one of the simplest forms of hydroids. Such an individual is certainly as low in organization as the Protohydra, Microhydra, and similar low genera which are destitute of tentacles.

This reduction in the form of the hydranth by the disappearance of the tentacles in Hydrichthys is believed to be a degeneration brought about by its life, and not, as in Protohydra, due to the low zoölogical position of the hydroid.† The character of the medusa of Hydrichthys and its resemblance to

* As this comparison is only in general external outlines, no account of the fact that the gonophores of Tubularia take the form of actinulæ, while those of Hydrichthys appear as medusæ, is considered. *En passant*, however, it might be said that morphologically the actinula and the medusa are thought to be homologous, as several naturalists have already shown. I regard both medusa and hydroid as a modification in different directions of an ancestral form which is most closely adhered to in a stage of the Siphonophores to which I have given the name "primitive larva," or "primitive medusa." Morphologically considered, a medusa and a simple hydroid are homologous, as shown by a study of Stephanoscyphus (Allman), Cunina, the young of Agalma as compared with the young Nanomia, and other genera. This identity, in a morphological way, of medusa and hydroid has long been recognized, and was pointed out many years ago by Claus and others.

The egg in its development may pass into one or the other of these homologous stages. It may become fixed to a submarine object, and become a fixed hydroid; it may pass into a free medusa or medusiform condition homologous to a hydroid, as in Glossocodon or in Agalma; or it may be developed into a parasitic Hydrichthys. It seems probable that, as I have already elsewhere shown, the attached form of the medusa or the hydroid is a secondary condition, and that the primary condition is a direct development from the egg to the adult medusa. I would regard the ancestral form of metagenesis to be the development of the "primitive medusa," from an organism with both hydroid and medusan affinities, directly from the egg without attachment. From that medusa, — which I would call and have elsewhere named the primitive medusa, — in some instances, free medusiform gonophores bud, as in Agalma; in other cases, the primitive medusa becomes attached, and is modified into a hydroid from which free gonophores separate; while in still other cases, Nanomia, the primitive medusa is neither medusiform nor attached hydroid-like, but planula-like, with a float. The primitive medusa is homologous in all these changed forms.

† There is no reason to suppose that non-tentaculated genera allied to Hydra

Sarsia shows that the affinities of the genus are higher than its hydroid would seem to indicate. There is a pretty close likeness between most of the hydroids of the medusæ to which the Hydrichthys medusa is allied. This radical departure in Hydrichthys in the form of the hydroid itself may have a meaning, and the exceptional anatomy is thought to be due, at least in part, to its parasitic life, especially as the medusa is so closely allied to other tubularian medusiform gonophores. In the development of the egg of Hydrichthys, it is supposed that the planula, instead of fastening itself to some submarine object, becomes attached to the fish. The necessities for the development of tentacles would be reduced from the fact that the fish (Seriola) carries the hydroid about, and perhaps furnishes sustenance for the parasite from its own body. As a result, the hydroid suffers a degeneration, or remains in a degraded condition.

The needs of procreation, however, still remain, and the necessity for the locomotion of the sexual zoöid and the organs for the development of new individuals is in no way diminished by the parasitic life of the hydroid. Instead of being reduced in size, they are, if anything, enlarged in number ; and as the medusiform gonophore separated from the gonosome is placed under exactly the same conditions as that of any fixed hydroid, it retains characters of its near relatives.*

Hydrichthys has certain features in the anatomy which recall the floating hydroid, Velella. The gonosomes resemble in several particulars the sexual bodies of Velella, and the free medusa is not very different from Chrysomitra, the medusa of Velella. The flat basal disk also of Hydrichthys has points of resemblance to the basal plate and the ramifying tubes on the under side of the float in the well-known *V. spirans*. In the polymorphism of the two there is some likeness. In Velella we have a single non-tentaculated "central polyp," or polypite, surrounded by many sexual bodies, or gonosomes. We have in Velella, moreover, two kinds of individuals, which is perhaps the simplest kind of polymorphism anywhere known among Siphonophores, except in the kindred genus Porpita. In Hydrichthys we also have two

ever have a free medusiform gonophore. They probably have a development like Hydra, and are destitute of special locomotive zoöids.

It is, of course, an open question whether Hydra and Protohydra are nearer the ancestral type than other hydroids. It is not unlikely that they are degenerate forms, and not ancestral. The peculiarities of their habitat in fresh water might have led to their low zoölogical position. As a question of opinion, the author regards them as phylogenetically low, and nearer the ancestral form of hydroids than Syncoryne and others.

* Those who have studied the Hydromedusæ have for the most part based their classifications either on the form of the hydroid, or the form of the medusiform gonophore. Both are in error if they rely upon either hydroid or medusa alone as a basis of classification. Hydrichthys certainly shows that this is true ; for, if known from the hydroid alone, it might be placed in a zoölogical position very far from that which its medusa would indicate as its true one.

kinds of individuals: the gonosomes, which are similar to the sexual individual of Velella, and the "filiform bodies," which closely resemble the central polypite of Velella and Porpita. If this likeness between the parasitic Hydrichthys and the free-swimming Velella is a morphological one, it may throw new light on the relationship of the hydroids and Siphonophores. The parasitic nature of the life of Hydrichthys leads us to compare it with the strange Cœlentrate organism, *Polypodium hydriforme*, also parasitic, described by P. Owsjannikow,* and later by O. Grimm,† in the ova of Acipenser. The resemblances between the two are, however, of a most distant kind, and the affinities of the two are slight.

The only stage in the life history of Polypodium which can be homologized with Hydrichthys is the hydroid stage, the cylindrical hollow tube covered by buds. This is the spirally twisted tube with numerous lateral appendages, figured by Ussow ‡ in Figs. 1–5. If we suppose the hydroid of Hydrichthys to have the lateral branches reduced in size, the buds brought to the side of the main axis, and the main axis itself closed at either end, flexible, and motile, we should have something similar to what exists in the first stage of Polypodium, found in the egg of the sturgeon. I cannot, however, believe that the likeness is very close between them, although the form of both is undoubtedly due, in part at least, to their parasitic life on the animals with which they are associated.

When we come to compare the organism formed from Polypodium by the breaking up of or budding from the stem, and the relatively highly organized Sarsia-like organism (medusa) derived from Hydrichthys, we find little likeness between them, judging from the figures of Polypodium given by Ussow, and my own. I am therefore convinced that the affinities of Hydrichthys and Polypodium are very remote, and that parasitism has affected them in very different ways,§ so far as the modifications in their anatomy are concerned.

Turris episcopalis, Fewkes.

This beautiful medusa was found in great abundance at North Head, Grand Manan. The few specimens of this genus which have been found at New-

* Arbeiten der dritten russischen Naturforscherversammlung in Kiew. Reference: Zeit. Wiss. Zoöl., XXII. 292; Mélanges biologiques de l'Acad. des Sci. de St. Pétersbourg, 1871.

† Arbeiten der Naturforschergesellschaft zu Petersburg, 1873.

‡ Morphologisches Jahrbuch, XII. 137–153; Ann. Mag. Nat. Hist., XVIII. 110–124, Pl. IV. It is of course not impossible that Hydrichthys may be a transition form between true hydroids like Tubularia and Syncoryne on the one hand, and the extremely modified genus Polypodium on the other. The author does not deny this possibility, although the relation of the two is distant.

§ The amount of modification in the structure of Polypodium would naturally be very much greater than in Hydrichthys, on account of its peculiar habitat inside the fish.

port, R, I., from one of which the type was described, are evidently stragglers from cold water, where they are abundant, and not from the warm waters of the Gulf Stream, from which they have yet to be taken.

Melicertum campanula, Esch.

This large and beautiful medusa is one of the most common at Grand Manan.

Specimens of the young in all stages of growth were easily collected. These are found to have been well described by Agassiz, and nothing of value was added to his observations.

Nemopsis* bachei. Ag.

Staurophora laciniata, Ag.

This beautiful medusa is common at Grand Manan. It grows to a large size, and is one of the most conspicuous genera in sheltered bays near the north end of the island. I have also found several large specimens of Staurophora at Frye's Island, New Brunswick.†

Halopsis ocellata, A. Ag.

Plate III. Fig. 1.

The genus Halopsis was found quite abundantly near the wharfs at Grand Manan. The specimens which were taken differ somewhat from the figures and description of the type, but evidently belong to this species.

The bell, in several specimens, is from four to six inches in diameter. Its walls are thick, without apical prominence. The radial canals arise regularly,

* Sometimes erroneously written Mnemopsis. The derivation is νῆμα, tentacle, and ὄψις. The use of the wrong spelling is liable to lead to confusion with the Ctenophore, Mnemiopsis.

† In the surface fishing at Frye's Island, New Brunswick, several interesting larvæ were found with Staurophora. Among these were many specimens of the singular worm larva, Mitraria. These larvæ were taken in great abundance in July, and were generally captured with the Müller net in night fishing. In Narragansett Bay, Mitraria is not found. The problematical affinities of this singular worm larva, and its abundance in Passamaquoddy Bay, would seem to invite naturalists to observations upon its development.

Swarms of an Appendicularia different from that found at Newport were also observed at Grand Manan and Eastport. The body of the Grand Manan Appendicularia is larger than the Newport, and more dumb-bell-shaped, the tail arising from the middle of the body.

not in four groups,* from the stomach cavity. Sexual glands are situated ordinarily as described, but often have a bright pink color instead of white.

Otocysts large, compound, as already described in Halopsis by A. Agassiz. This medusa is very abundant at Eastport, Me., as well as at Grand Manan,† where it seems to occur during the whole summer. No subject would better repay investigation than that of the histology of the "compound eyes." or otocysts, of Halopsis.

Oceania languida (Ag.),‡ A. Ag.

An Oceania similar to *O. languida* was found in abundance near Eastport, Me. A few specimens occurred at North Head, Grand Manan.

Obelia, sp. ?

An unidentified Obelia is common at Grand Manan.

DISCOPHORA.

Cyanea arctica, Per. et Les.

Nowhere on the Atlantic coast, except at Eastport, Me., have I seen such magnificent specimens of this medusa as near the landing-place at North Head, Grand Manan.

Aurelia flavidula, Per. et Les.

The *Aurelia aurita* described by Stimpson from Grand Manan is evidently, as already pointed out by A. Agassiz, the *A. flavidula*, Per. et Les. Specimens were found at North Head in considerable numbers, and of great size.

Callinema, Verrill.

Plate VI.

Since its discovery at Eastport by Prof. A. E. Verrill, the interesting genus Callinema has not been studied, although Eastport has been repeatedly visited

* In this respect my specimens differ from the type.

† This is thought to be the first mention of Halopsis from localities north of Massachusetts Bay, on the New England or New Brunswick coasts.

‡ Name *languida* used by L. Agassiz in 1862 in "Contributions to the Natural History of the United States." A special description of *O. languida*, with figures, is to be found in "North American Acalephæ," by A. Agassiz. The specimens studied closely resemble the types.

by naturalists. No additions worth mentioning to our knowledge of this extraordinary genus has been made since Verrill's original paper. Prof. Verrill collected Callinema on two different occasions, and he records that he found three specimens in all. In the summer of 1885, I also found this jelly-fish among the Eastport wharves, and took a single specimen.

My specimen of Callinema was collected under most unfavorable circumstances. The water was very rough, and it was with great difficulty that I succeeded in capturing the medusa and bringing it on shore. When the genus was first seen it was mistaken for a Cyanea, and before its capture it was regarded as a new specimen of Zygodactyla. It was only later, when brought on shore, that it was possible for me to detect its true relationship, and to establish its identity with the rare Callinema.

This genus is one of the most extraordinary found on the New England coast. It is believed that an extended account of its anatomy is necessary, not only to show how distinct it is from a Pacific Ocean relative, *H. ambigua*, but also to afford a means of comparison and determination of the systematic position of a Mediterranean ally, called by Haeckel *Phacellophora sicula*.

The original description* of Callinema by Prof. Verrill is concise, and leaves no doubt as to the form of the more important organs of his genus. Unfortunately, his account is unaccompanied by figures, so that some details of structure need illustration to render his description clearer. Since my rediscovery of Callinema, Prof. Verrill has sent me woodcuts representing portions of the disk and tubes, and part of a tentacle, so that I can easily follow his written description as far as these organs are concerned. There is, however, still believed to be a call for the publication of figures of the medusa as a whole, to show the relationship of the parts. In the present description I have simply tried to emphasize certain details of structure, barely touched upon in the original accounts, and to figure the outlines of the medusa as a help to future investigators.

Callinema ornata, Verr.

Disk (Figs. 2, 3) flat, thick, with rounded apex, fourteen inches in diameter.† The margin of the bell hangs downwards when the medusa is in motion. The external surface of the bell (Figs. 1, 2) is covered with small

* Description of a Remarkable New Jelly-fish, and two Actinians, from the Coast of Maine. Am. Journ. Arts and Sci., Vol. XLVIII. pp. 116–118. See also Ann. Mag. Nat. Hist., Vol. IV. p. 161.

Haeckel (System der Medusen Acraspeden, p. 643) prints a condensed notice of Callinema, under the name Phacellophora, but does not mention Prof. Verrill's *original* description in the American Journal. Verrill's description in the "Annals and Magazine of Natural History," used by Haeckel, is, however, the same as the original account.

† One of Verrill's specimens was eighteen inches in diameter and another ten.

warts or papillæ. Walls of the bell transparent, with conspicuous radiating tubes.

The radial tubes (Fig. 3) are of two forms: those which lie in the radius of the sense bodies, which are more or less anastomosing and branching; while those in intermediate sphærosomes are unbranched, straight, and almost parallel with each other. Tubes broad, slightly brown color, extending from the stomach cavity to the marginal vessel. There are sixteen sets of anastomosing tubes and the same number of unbranched vessels. The former lie in the radii of the sense bodies of the bell margin. The marginal vessel is continuous, obscurely sinuous, broad, without lobes.

There are sixteen hooded (Fig. 5, *v*) sense bodies on the bell margin. Each marginal sense body (*o*) is pearl-white and conspicuous. The intimate structure is like that of *P. sicula*, described by the Hertwigs.* The rim of the bell between each pair of marginal sense bodies (Figs. 4, 5) is filled by a broad lobe (*a*, *b*), the margin of which is indented and incised or scalloped. The sixteen marginal lobes are separated by deep incisions, at the deepest part of which lie the marginal sense bodies. The marginal lobes are penetrated by blindly ending vessels or tubes (*cr*), which arise from the circular tube (*cl*) between and among the tentacles. These blind tubes of the marginal lappets are sometimes slightly bifurcated at the end, and sometimes send off small lateral serrations. They are never branched, nor anastomosing. The tube which arises from the marginal circular vessel in the radius of the otocyst divides into three divisions shortly after it leaves the point of origin. The median, or smallest of the three divisions, extends into the cavity of the style of the otocyst (*o*). The two lateral divisions (*ch*) are somewhat bow-shaped and follow along the side of the cleft in which the margin of the bell is incised for the otocyst. The cavity of the two bow-shaped divisions (*ch*) is entire on the inner border, and more or less serrated on the side turned toward the marginal cleft in which the otocyst lies.

The tentacles (*p*) are numerous, and arise, not from the edges of the marginal lappets, but from the neighborhood of the circular marginal vessel (*cl*). The tentacles vary very greatly in size, and are placed side by side (Figs. 3, 4) along the circular tube into which, alternating with the marginal vessels, they open. Each tentacle is long and somewhat flat, with a finely scalloped double edge of white color. There are from eight to ten tentacles between each pair of marginal sense bodies.

The mouth lobes (*ga*) resemble those of Cyanea, and consist of folded curtains of yellow and brown color. The walls of the actinostome are more or less extended outward (Fig. 1), and the lips are entire.

There are eight large sexual bodies (*sp*) hanging at the base of the mouth parts near their attachment. These structures are prominent and have a brownish color. The sexual filaments are large and conspicuous.

No other species of Callinema, or of the closely allied Phacellophora, has

* Nervensystem und Sinnesorganen der Medusen, pp. 113, 114.

been taken in the Atlantic or in the Mediterranean, with the exception of the problematical *P. sicula*, Haeck., from Messina.

In his original description Prof. Verrill suggests that Callinema is allied to *Heccædecomma ambiguum*, Brandt, of the North Pacific, but finds that the Eastport species differs from the Pacific in the shape and character of the tentacles, the marginal lobes, and ovaries, and that the figures of the Pacific form have much more complicated mouth-folds. I agree with Professor Verrill in his conclusions in regard to the differences between the two medusæ, and find his medusa specifically different, not only from the published figures of the Pacific Phacellophora, but also from specimens themselves, some of which were collected on my recent visit to the Pacific coast. It is also believed to be generically different from Heccædecomma.

Haeckel* suggests that Callinema is a new species of Phacellophora There are close likenesses between Callinema and Phacellophora, and also differences which seem great enough to give the name Callinema a generic worth. Haeckel, however, regards these differences as specific only, and regards Callinema as a new species of Phacellophora. In the same genus he places three other species, *camtschatica*, Brandt, *ambigua*, Brandt, and *sicula*, Haeckel. I consider, as stated above, that there is a generic difference between Callinema and the first two species. Of the third species, from Messina, there are no special lescriptions, and no figures of the medusa as a whole, and we are wholly in the dark in regard to the structure of the mouth parts. What is known from the notices by the Hertwigs † — the figures are of a quadrant of the bell and an enlarged sense body — would lead me to suppose that his medusa is very close to Callinema. It would seem to be a species of Callinema allied to *C. ornata*. Until we know more of its general anatomy, we must remain in doubt whether it is more closely allied to Phacellophora or Callinema. I can heartily agree with Haeckel that an exact study of the structure of the medusa considered by Hertwig is very desirable. The author believes that histological researches lose some of their value if not preceded by an accurate specific identification or specific description of the animal studied, if it is different from known species.

* Das System der Medusen. Acraspeden, p. 643.

† Nervensystem und Sinnesorganen der Medusen, pp. 113, 114, Taf. IX. Fig. 15, Taf. X. Fig. 16.

CAMBRIDGE, October, 1887.

EXPLANATION OF THE PLATES.

PLATE I.

View of *Nanomia cara* (life size).

f.	Float.	*nc.*	Nectocalyx.
g.	Sexual bell.	*ns.*	Nectostem.
h ph.	Hydrophyllium.	*og.*	Oil globule.
ht.	Hydrocyst.	*p.*	Polypite.
h ta.	Tentacle of the hydrocyst.	*ps.*	Polyp stem.
k.	Retracted tentacular knob.	*ta.*	Tentacle.

PLATE II.

Nanomia cara, A. Ag.

c f.	Stiff projections at the distal end of the embryonic tentacles.	*inv.*	Involucrum of adult knob.
1 *cl.* 2 *cl.*	First and second cleavage planes.	*lc.*	Lateral nematocyst of the embryonic knob.
fl.	Terminal filament of the adult tentacular knob.	*og.*	Oil globule.
ht.	Hydrocyst.	*ped.*	Peduncle of the tentacular knob.
h ta.	Tentacle of the hydrocyst.	*pl.*	Protoplasmic elevation.
		sac.	Sacculus.

Fig. 1. Egg with the primitive furrow almost formed, showing superficial protoplasmic envelope and protoplasmic network.
Fig. 2. The same, a little younger.
Fig. 3. Two-cell stage.
Fig. 4. Four-cell stage.
Fig. 5. Four-cell stage turned in another plane.
Fig. 6. Beginnings of the furrows which form the eight-cell stage.
Fig. 7. Hydrocyst of Nanomia found detached from the parent stem.
Fig. 8. Embryonic tentacular knob.
Fig. 9. Adult tentacular knob.

PLATE III.

Fig. 1. Upper portion of a taster of Nanomia, showing the so-called oil globule forming a protuberance on one side. The tentacle is not represented

Fig. 2. Four nectocalyces of Nanomia, showing their mode of fitting together. The stem is shown through the sides of the "horns," or gelatinous extensions of the nectocalyx. The sinuous tubes are the lateral chymiferous vessels. The radial tubes, which pass directly, without a sinuous course, from the tube which joins the system to the stem, are not shown.

Fig. 3. *Halopsis ocellata* (side view).

PLATE IV.

Fig. 1. A fish (*Seriola zonata*) with Hydrichthys attached to its side and anal region.

Fig. 2. Single cluster of gonophores separated from attachment to the basal plate by which the whole colony is united to the fish. The attachment is at the lower end. Medusa buds in various stages of development are shown at the ends of the lateral branches. Each attached colony has a large number of bodies like Fig. 2 scattered irregularly on the basal plate. The structure represented in Fig. 2 is described as the gonosome of Hydrichthys.

Fig. 3. Single filiform body of a Hydrichthys colony.

Fig. 4. Section (optical) of a medusa bud of Hydrichthys. The two projections on the left are the opposite tentacles, which have an internal cavity communicating with radial tubes, two of which are represented. The two spurs from this cavity which arise near the bases of the tentacles are the beginnings of the circular canal. The large cavity at the centre of the bell is the cavity of the proboscis. The slit-like cavity separated from the cavity of the proboscis by the thick layer and the thin layer which lines the former, is the future bell cavity.

Fig. 5. Enlarged end of the filiform body of Hydrichthys, showing the orifice open and a round mass (food ?) in its cavity.

PLATE V.

Fig. 1. Adult medusiform gonophore of Hydrichthys with four tentacles (side view). This medusa was raised from the hydroid, and is supposed to be not much younger than the adult.

Fig. 2. An immature medusa of Hydrichthys found in the aquarium on the morning after capture. Raised from the Hydrichthys in countless numbers. (Side view.)

Fig. 3. View of the last-mentioned from actinostomal region. This medusa is a very little younger than Fig. 2, since the two stumpy tentacles have not yet begun to appear.

PLATE VI.

Callinema ornata, VERR.

a. Portion of the marginal lobe adjoining the marginal cleft in which the otocyst lies. The separation of this lobe from the remainder of the marginal lappet is indicated by a slight depression in the margin or rim of the lappet.

b. Intermediate portion of the marginal lappet between two indentations which separate it from *a*.

Of the two regions of the margin of the umbrella, *a* may be called the ocular lappet and *b* the velar lappet.

ch. Vessel arising from the marginal tube and blindly ending in the ocular lappet.

cr. Vessels of the same character as the last in the velar lappets.

cl. Marginal or circular chymiferous tube.

ga. Oral folds

o. Otocyst, or marginal sense body.

p. Tentacle.

sp. Sexual organs.

v. Hood over the marginal sense body.

Fig. 1. Side view of Callinema, bell contracted.

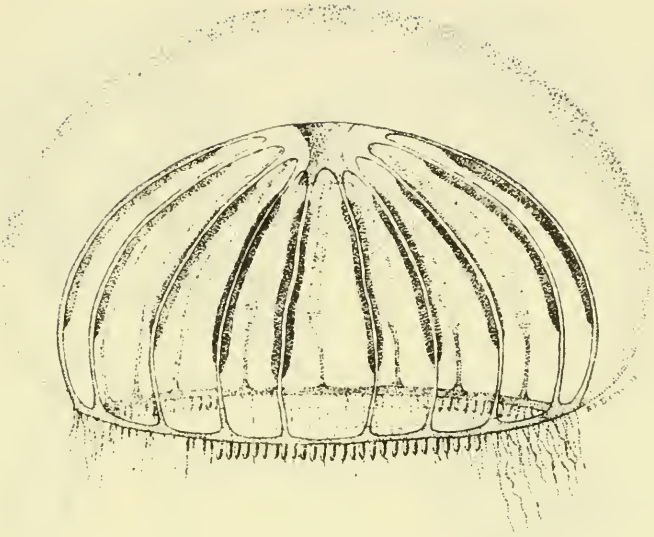
Fig. 2. Same, bell more expanded. (The tentacles are cut off in Fig. 2 and more or less retracted in Fig. 1. Half of the figure drawn in outline.)

Fig. 3. View of the anastomosing and unbranched radial tubes, seen from above. (Tubes drawn in a quadrant of the bell.)

Fig. 4. Section of the bell margin, including a velar (*b*) and an ocular lappet (*a*). This figure shows also the relative position of the otocyst, tentacle, and blind tubes of the marginal region.

Fig. 5. A section of the bell margin of the same specimen from which the last was drawn (shown from a different spheromere).

All figures except Fig. 1, Plate IV., were drawn from nature by the author. The pen and ink sketches of Plate III. Fig. 3, and of Plates IV. and V., were made by Mr. S. W. Denton. All the others are by the author.



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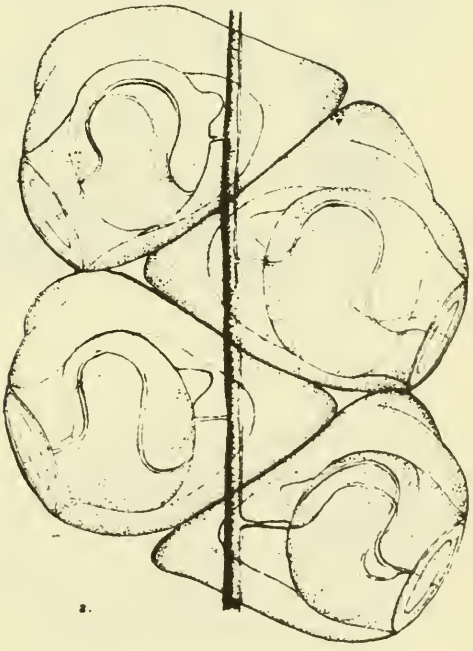

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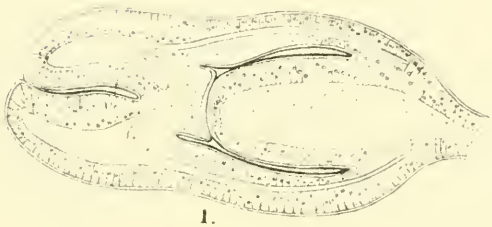

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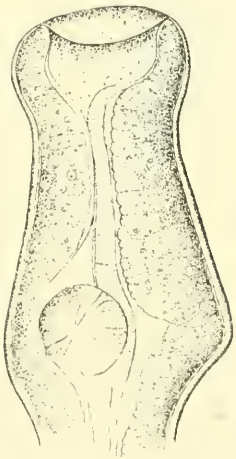

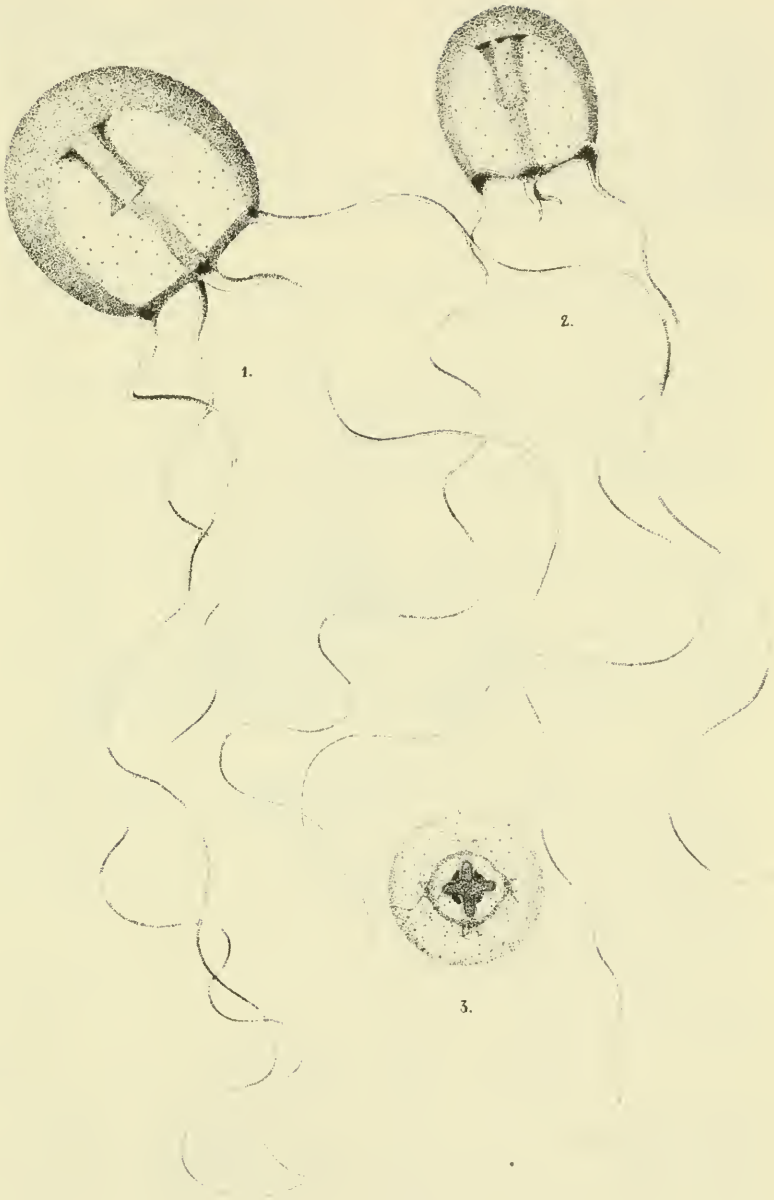
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These may be properly termed anterior and posterior tympanic vacuities, or foramina, corresponding to the *foramen lacerum medium* and *foramen lacerum posterius basis cranii* of anatomists. Plate II. Figs. 9, 10, *a*.

2. "Orbito-nasal" includes the vertical plate of the palatine, and the margins of the palatine, maxilla, alisphenoid, orbitosphenoid, and frontal, at their lines of juncture, as also the combination of certain foramina. Plate II. Fig. 7, *a*, *b*.

3. "Palatine" designates the anterior and posterior portions of the palate, one or both. Plate I. Figs. 1, 2, *a*, *b*.

4. "Facial" includes the side wall of the face, the latero-nasal portions of the maxilla, and the anterior root of the zygoma. Plate II. Fig. 8, *a*. Plate I. Figs. 3, 5, *a*, *b*.

5. The "Occipito-squamosal" is the space comprehended between the supraoccipital, exoccipital, and squamosal. Plate II. Fig. 11.

6. The "Squamosal" and "Parasquamosal" are indicated by the terms used. Plate I. Fig. 4, *b*.

The cranial vacuities in the various orders of the Mammalia occur as follows.

Monotremata. — The skull of the Echidna presents no vacuities. In the Ornithorynchus, there are relatively large anterior and posterior deficiencies, the first representing the foramen ovale, and the second the jugular and the præcondyloid foramina combined. There are also small ones in the basisphenoid.

Marsupialia. — Many of the Macropodidæ have large posterior palatine vacuities. These are present also in Phascolarctos (Plate I. Fig. 1, *a*), in the Dasyuridæ (Plate I. Fig. 2, *a*, *b*), and in the Peramelidæ. *Perameles lagotis* has a large oval vacuity which extends from the second premolar to the penult molar, and posterior to this are found several small ones. In the Didelphidæ there are large posterior palatine vacuities.

Edentata. — This order is singularly free from cranial deficiencies. In the Dasypodidæ the posterior tympanic vacuity, or *foramen lacerum posterius*, is somewhat enlarged. Among the Sloths, *Cholœpus hoffmanni* presents considerable deficiencies in the basi-sphenoidal region.

Chiroptera. — In a few genera, notably in Pteropus, the posterior tympanic vacuities are large.

Insectivora. — In some of the Erinaceidæ, the post-tympanic are large, while there are also extensive post-palatine vacuities, especially in *Erinaceus europœus*. In Sorex, large latero-basal ones are found, and Tupaia has a large longitudinal central deficiency of the malar, in addition to the palatal vacuities.

Rodentia. *Lagomorpha.* — In the Hare, at the posterior portion of the inter-orbital septum, the foramen, which serves as a common outlet of the optic nerves, is sufficiently enlarged to constitute a vacuity. There are also large vacuities extending from each orbit into the latero-nasal regions; these being covered externally by the singularly reticulated plate of the maxilla. (Plate I. Fig. 3, *a*, *b*.) Pre- and post-palatine deficiencies reduce the palate itself to a mere narrow bridge extending across between the premolars.

Sciuromorpha. — In the Sciuridæ, there is a small orbito-nasal deficiency. In *Castor fiber* there are large anterior tympanic spaces.

Myomorpha. — The anterior root of the zygoma presents a vacuity in very many of the Rodentia (Plate I. Fig. 4 *a*), and in the Rats generally this is vertical and dilated superiorly. In *Fiber zibethicum*, the malar vacuity is large, and there is also one in the posterior process of the squamosal (Plate I. Fig. 4 *b*), which is also present in several of the Muridæ. In Lagostomus, a thin bony plate separates the infra-orbital foramen from the antorbital vacuity.

Hystricomorpha. — In the Porcupines generally, and especially in *Erethison dorsatus*, the infra-orbital as also the ante-tympanic vacuities are large. In the Capybara, the former is immense. In Chinchilla a large deficiency also occurs in the parasquamosal region between the alisphenoid, parietal, and tympanic. (Plate I. Fig. 5, *a*.) In Paca, the foramina, rotundum, and *lacerum anterius* combine to form a capacious orbito-nasal vacuity.

Carnivora. Pinnipedia. *Phocidæ.* — Large latero-posterior basal deficiencies occur in all, while in some, as in *P. vitulina*, *P. grœnlandica*, and *P. fœtida*, there is in addition to these a more or less extensive perforation in the basioccipital. (Plate I. Fig. 6, *b*.) In the orbito-nasal region, not only is the spheno-palatine foramen much enlarged, but a deficiency occurs at the juncture of the maxilla, palatine, and frontal, often attaining a large size. (Plate II. Fig. 7, *a*.)

Otariidæ. — The *foramen lacerum posterius* is much enlarged, while the orbito-nasal vacuities are extensive, in this family. In Zalophus and Callirhinus, in addition to the above, there are large vacuities at the juncture of the vertical plate of the palatine with the alisphenoid and orbitosphenoid. (Plate II. Fig. 7, *b*.)

Rosmaridæ. — In the Walruses there are large orbito-nasal and posterior tympanic vacuities, while the anterior root of the zygoma is largely dilated.

Fissipedia. — In this sub-order, with very few exceptions, no vacuities

occur. In Enhydra (Sea Otter) the post-tympanic fissure is large; there is also an orbito-nasal deficiency. The infra-orbital opening is capacious.

Ungulata. Artiodactyla. — In many of the Ruminants, as in the Cervidæ, Camelidæ, Antilocapridæ, and in some of the Bovidæ, as in Antilopinæ and Caprinæ, a large facial vacuity exists at the juncture of the frontal, lacrymal, malar, and nasal bones, which leads into the nasal cavities. (Plate II. Fig. 8, *a*.) Where the upper incisors are entirely absent, the anterior palatine foramina assume large proportions, becoming veritable deficiencies. In some of the Cervidæ, as in Rangifer, Alces, and in Antilocapridæ, a more or less extensive orbito-nasal vacuity exists at the juncture of the vertical plate of the palatine, alisphenoid, and lacrymal. In Suidæ and Dicotylidæ the *foramen lacerum medium* is large, and in Hippopotamidæ both ante- and post-tympanic foramina are capacious.

Perissodactyla. — In the Equidæ, the anterior and posterior tympanic foramina with the ovale combine to form an extensive deficiency in the postero-lateral basal region. (Plate II. Fig. 9, *a*.) In the Rhinocerotidæ, the foramina, ovale, and *lacerum medium* are combined. There is also a considerable orbito-nasal vacuity, as well as one formed by the combination of the two anterior palatine foramina.

In Tapiridæ, the anterior, posterior tympanic foramina, and the ovale are joined, as also are the anterior palatine, as in the Rhinocerotidæ.

Sirenia. — In the two genera Manatus and Halicore, which constitute the present order, the entire latero-posterior basal region, between the occipital and alisphenoid, may be considered as a vacuity, so imperfectly is it filled by the tympanic and periotic. (Plate II. Fig. 10, *a*.) In the later-ooccipital region, at the juncture of the squamosal with the supraoccipital and exoccipital, a large vacuity also exists, very imperfectly filled by the periotic. (Plate II. Fig. 11, *a*, *b*.) The dilatation of the supraorbital foramen is also large, and there are extensive orbito-nasal openings.

Hyracoidea. — In Hyrax, the anterior tympanic deficiency is relatively large.

Proboscidea. — In the Elephant, the tympanic deficiencies so uniformly present in the odd-toed Ungulates can scarcely be said to exist.

Cetacea. — In the Odontoceti, and notably in the Delphinoidæ, large irregular openings exist between the recess which holds the united tympanic and periotic and the cranial cavity. The optic foramen, as it passes out through the orbito-sphenoid, is much enlarged, being

converted in some instances into a vacuity. Upon the latero-external walls of the posterior nares large oval notches or deficiencies occur.

PRIMATES. — The sphenoidal and sphenomaxillary fissures in man, as also the *foramen lacerum medium*, which is often very large and irregular in shape, come under the second category of vacuities. The same also applies to the anterior tympanic of the higher Apes.

In studying the etiology of these cranial vacuities in the Mammalia, it would seem at first sight, especially if the imperfect osseous condition of the skull in many of the lower Vertebrates be taken into consideration, that their existence was due to phylogenetic degeneration, taken in the widest acceptation of the term. A closer study of the conditions presented, however, apparently limits this degeneration to one of environment. Take as an illustration the Pinnipedia, in which group the economy of nature as regards the disposition of material is admirably shown. These true Carnivora have become adapted to an existence in water. Consequent changes suited to this aquatic life have been undergone. The thick skull of the Fissipedia is no longer necessary; consequently the cranial walls have become much thinned, and several large and extraordinary vacuities in different regions, notably in the basal, have been formed.

A reduction has taken place in the number and strength of the teeth, and other characteristics of the order have been materially altered or entirely lost. These changes have been foreshadowed in the Enhydra (Sea Otter), as has already been noted.

So also any diminution in the strength of the cranial walls of the ancient branch of the Ungulata, the Sirenia, due to large deficiencies, is counterbalanced by the aquatic habits of the order.

In the Rodents, the alveolar border of the maxilla is pushed far back, and thus the unoccupied space between the incisors and premolars is relatively large. This absence of teeth necessitates only a small supply of bony material in the immediate region, so that in the case of the Hare, which feeds upon a succulent diet, little strength or resistance is demanded, and consequently large vacuities are found in the latero-nasal region. The nasal plate of the maxilla is rendered lighter by the reticulation, which may be considered as a series of small vacuities, while it still serves as a protection to the delicate structures beneath. Again, the presence of the vacuity in the side-walls of the face in many of the Ruminants, and in consequence the apparently weakened condition of the parts, may be explained by the statement that either the animal is of so peaceful a nature that consolidated bones such as the frontals

of the Bovinæ are entirely unnecessary, or, being combative, provision is made for purposes of offence and defence by the growth of antlers or other horns.

Thus, without further illustration, it may be said, that while it is difficult in the present state of our knowledge to account for the varied character and position held by cranial vacuities, or to explain why these should be more frequently present in some orders than in others, and in certain genera of an order and not in others, it may nevertheless be safely affirmed that whenever osseous material can be set aside without interference with the general economy, or without detriment to the structure of the immediate parts, it is dispensed with. This general law applies to all vacuities or deficiencies, wherever situated, in the crania of the Mammalia.

Cambridge, January, 1888.

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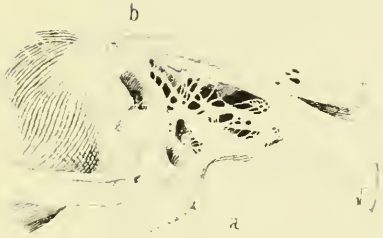

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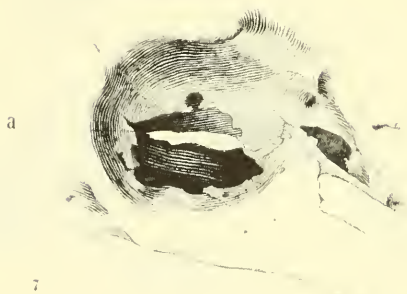
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No. 9. — *The Superior Incisors and Canine Teeth of Sheep.* By Florence Mayo.*

In 1839 Goodsir (p. 83) stated that "the cow and sheep, and probably all the other ruminants, possess the germs of canines and superior incisives at an early period of their embryonic existence."

This statement remained undisputed until 1873, when Pietkewickz (p. 509) denied the existence not only of the teeth germs, but also of the so-called dental lamina. He says: "Dans une longue série de preparations faites sur des embryons de boeuf et de mouton, pris depuis le moment le plus reculé de la vie embryonnaire jusqu'à une longuer de 30 centimetres, non seulement je n'ai jamais constaté la présence de follicules, mais je n'ai même jamais trouvé trace de la lame épitheliale."

Legros and Magitot ('73, p. 452) content themselves with simply quoting the results attained by Pietkewickz, but add nothing of their own.

Somewhat later, Piana ('78, p. 222) asserts that the epithelial lamina of the upper jaw extends to the region where the lateral incisors ought to develop, and that the enamel germs of the canine teeth exist at a certain stage of development, but soon abort.

Pouchet and Chabry ('84, p. 158), calling the canine tooth the fourth incisor, admit the existence of a dental lamina in the region of the upper jaw, which is directly over the second incisor of the lower jaw, but claim that in front of this point it becomes gradually merged into the crest of the plunging wall. They add: "Ainsi non seulement la région incisive des ruminants ne présente aucun vestige de dents, contrairement à ce qu'on avait cru à une certaine epoque, mais elle ne possède pas même de lame dentaire differentiée, dans toute son étendue."

In view of these conflicting statements and the theoretical interest of the questions involved, further studies upon the subject are desirable. Therefore, at the suggestion of Prof. E. L. Mark, and under his direction, I have undertaken to re-examine the development of the teeth in sheep embryos of different ages, hoping to be able to add something to what was already known. My observations are as follows: —

* Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the Direction of E. L. Mark. — No. XIII.

The jaws of a sheep embryo whose length was 37 m.m. were sectioned so that the plane of the first section was parallel to the median plane of the jaw. After a small number of sections had been cut parallel to this plane, the object was slightly rotated, so as to keep the plane of the sections nearly perpendicular to the outer margin of the jaw. By thus frequently changing the plane of cutting, each section of the series was a true cross-section of the part of the jaw from which it was taken. This method of cutting must give more satisfactory results than can be had by cutting either parallel or perpendicular to the median plane of the jaw without any change in direction.

In the first of the sections of the upper jaw, in the region which corresponds to the first incisor of the lower jaw (fig. 1), the dental lamina is not distinct from that portion of the buccal epithelium which Pouchet and Chabry ('84, p. 152) have called the "mur plongeant." But before the first incisor of the lower jaw has been passed, and in the region of the second and third incisors (figs. 2, 3, and 5), the dental lamina, although not sharply marked off from the "plunging wall," is readily distinguishable from it. By comparing figs. 1 and 3, one finds that the epithelial tissue in fig. 3 sinks deeper into the mesoderm than in fig. 1; that the deep portion forms an angle of about 45° with the axis of the plunging wall in fig. 1; and that the width of this deep portion, that is, the distance from the base of the malpighian layer on one side, to the base of the same layer on the other side, is less than the width of the plunging wall in fig. 1. In fig. 3 the dotted line is introduced to show where the boundary of the plunging wall, as it appears in fig. 1, would fall if it were "projected" on to the plane of this section. This deep portion beyond the dotted line, although continuous with the plunging wall, and not histologically different from it, I believe to be, both by reason of its size and its direction, the most anterior indication of the dental lamina. In the sections through the canine region of the same jaw (fig. 7) the conditions of the dental lamina and plunging wall are the same as in the incisor region.

Dursy ('69) gives drawings of several sections through the incisor and canine regions of a sheep embryo at about the same stage as the one just described. He says (l. c., p. 214): "Taf. III. Fig. 1–8 zeigt die Zahnfurche mit dem Schmelzkeim von einem Schafsfötus, dessen Gaumen im Schliessungsprocess begriffen war; auffallend daran ist die Weite der Furche und daher auch die Breite der hellen Kernmasse des Schmelzkeims an *allen* Schnitten, die somit an den zahnlosen Stellen beim Schafe um diese späte zeit noch vorhanden ist." Dursy evidently

disregards the existence of the dental lamina and calls it the enamel germ, of which at this stage I find no trace. He also figures (Taf. III. Fig. 1–9), as existing throughout the incisor and canine regions, an area — or, as Tomes calls it, a "halo" — in the mesoderm which in his opinion always precedes the development of the dentine germ, and is probably caused by a concentration of mesodermic nuclei. I have been unable to find, in any of the stages of development, this halo existing in any region of the upper jaw farther forward than that of the first premolar. The only indication of such a condition has been a slightly increased concentration in the nuclei immediately surrounding the epithelial germ, which, however, is hardly more pronounced than in the mesoderm which abuts upon neighboring portions of the buccal epithelium, and which is never sharply marked off on the deep side from other concentrations of nuclei which presage the formation of cartilage in the deeper mesoderm.

In an embryo 56 mm. long, cut in the same manner as the one just mentioned, the dental lamina is present *throughout the incisor region.* When studied with a low magnifying power (× 33), the sections through a part of the region of the first incisor, as in the younger stage, show no differentiation of a lamina from the plunging wall (figs. 11–14); but when a higher power is used (× 175), the malpighian layer of that portion of the plunging wall from which the lamina ought to proceed, is found to present an irregular outline on the side toward the mesoderm (fig. 30, *l. lng.*). It is no longer a layer one cell deep, but is composed of irregularly arranged cells, several deep. In the sections further back, behind the middle of the first incisor, and throughout the remaining incisor region (figs. 15–19), the dental lamina can be distinguished from the plunging wall by its size and direction. Its malpighian layer on the lingual side has undergone the same change as that just described in the region of the first incisor. The histological condition of the lamina in this region is identical with that which is presented at an early stage of development by the lamina, in regions where teeth are normally produced.*

* I find that the two walls of the dental lamina in the premolar region of the upper jaw, and in the incisor, canine, and premolar regions of the lower jaw, are histologically different. Pouchet and Chabry have mentioned this fact (pp. 154–155), and have given the names "adamantine" and "abadamantine" to the two walls of the lamina; but they do not state what the structural difference is. I have found that the malpighian layer of the lingual wall of the lamina is several cells deep. These cells are prismatic in form, and are compactly though irregularly

The fact that the dental lamina in the region of the second and third incisors is directly continuous with the differentiated portion of the plunging wall in the region of the first incisor, and has the same histological characteristics as that portion, seems good reason for believing that the latter is the representative of the dental lamina, which in this region never becomes further developed; whereas in the region of the second and third incisors it has become prolonged, and has changed its direction, owing to the multiplication of its undifferentiated cells.

In the canine region (fig. 20), the dental lamina at the place of its connection with the plunging wall has become very narrow. Its width at this point is very little more than the combined width of the two malpighian layers which form its walls, the corneous layer of epithelium being at this stage almost imperceptible. The deeper portion of the lamina by its enlargement has given rise to an enamel germ, which, although much smaller than the corresponding germ on the lower jaw, has the same histological characteristics.

The next stage studied was that of an embryo 87 mm. long. The lamina in the region of the first incisor (fig. 21) seems neither to have advanced nor to have retrograded in development from the condition in the embryo 56 mm. long. In the region of the remaining incisors (figs. 22, 23) the walls of the dental lamina have become thicker, and the corneous layer of epithelium forming its centre has undergone the same change as in the centre of the canine enamel germ of the preceding stage, — the cells are smaller and less regular in shape. In the region of the third incisor (fig. 31) the differentiated portion of the dental lamina, together with some of the unmodified portion, has begun to separate from the buccal epithelium; the mesodermic tissue by its ingrowth occupies for some extent the region which in earlier stages was uninterrupted epithelium. Although in this condition the lamina has a comparatively broad connection with the plunging wall, sections through the posterior portion of the incisor region show it entirely

arranged. On account of this irregularity the layer is in some places broader than in others, and presents an irregular outline on its mesodermic side. The labial wall of the lamina is histologically unchanged from the malpighian layer of the buccal epithelium. It is one cell deep, and has an even outline on the side toward the mesoderm.

The lingual wall increases in extent as the result of cell multiplication and forms the base of the enamel organ. Since the cells of the base of the enamel organ surround the dentine germ and at length produce the enamel, it is obvious that the lingual wall of the lamina produces, first, the enamel organ: and finally, the enamel.

surrounded by mesoderm. Throughout the regions of the third incisor and the canine tooth, small portions of the unchanged dental lamina are becoming separated from the epithelium. The corneous cells forming the centre of these small epithelial projections become vacuolated, and probably disappear, leaving only the cells of the malpighian layer, which, upon separating from the buccal epithelium, and becoming embedded in the mesoderm, form insulated masses or knots, which at this stage are very numerous. I have found an occasional knot of this kind in other regions of both jaws; but nowhere else have I seen so many as in the regions just mentioned. Since similar knots or islands appear during the degeneration of the neck of the enamel sac, I judge that they are all produced by the active ingrowth of mesodermic tissue, and are to a certain extent indications of a regressive development on the part of the dental lamina.

Piana (p. 220) likewise believes that the disappearance of the dental lamina in later stages is accomplished by its transformation into such islands. Legros and Magitot (p. 469) also describe similar epithelial knots, which are the remains of the dental lamina in the ordinary development of teeth. Although the epithelial knots found in the anterior portion of the upper jaw at this period are analogous to those found where the enamel organ is well developed, they differ from the latter, since when first formed they consist of prismatic cells from the malpighian layer. These cells gradually assume a more rounded shape, and the knots finally become lost in the surrounding mesodermic tissue; whereas the knots described by Legros and Magitot, although buds from the malpighian layer of the lamina, are claimed by them never to be made up of prismatic cells, as is that layer, but of small polyhedral cells which resemble those in the centre of the lamina at an early stage. The difference in appearance of these two kinds of epithelial knots is due, I believe, to the fact that those in the superior incisor and canine regions are the result of the rapid breaking up of the dental lamina, which quickly sets them free from the buccal epithelium; whereas those in the region of normally developing teeth are formed more slowly, and probably as the result of a more active cell proliferation on the part of the epithelium.

In the canine region also (fig. 32) the enamel germ is losing connection with the plunging wall, owing to the ingrowth of mesoderm, and is slightly larger than the germ in the embryo 56 mm. long.

In an embryo 93 mm. long the dental lamina has increased in size (figs. 34, 35), but, aside from a more marked difference between the

labial and lingual walls, it is not histologically different from the condition in the embryo whose length was 87 mm. In the canine region (fig. 33) the enamel germ has increased in size, and has sunk deeper into the mesoderm. The epithelial islands now consist exclusively of somewhat rounded cells from the malpighian layer, the corneous epithelium having disappeared from them. These knots by their juxtaposition form an almost unbroken series between the enamel germ and the epithelial plunging wall.

When the embryo has become 112 mm. long, the dental lamina in the region of the first incisor cannot be distinguished from the plunging wall. The cells of both the corneous and malpighian layers, which in younger stages had become differentiated, have again attained the condition of those of the plunging wall. In the region of the lateral incisors (fig. 36) the dental lamina, though yet distinguishable, has become much smaller and sinks less deeply into the mesoderm. Its differentiated cells have decreased in size, — cells from the malpighian and corneous layers closely resembling each other, — and its boundaries are less easily discernible on account of the greater irregularity in the arrangement of the malpighian cells. The enamel germ of the canine tooth (fig. 37) has become at this stage much diminished in size, and its cells are less specialized than in the preceding stages. Several of its central cells appear vacuolated, and this suggests an explanation of the manner in which it has suffered a reduction in size.

From the preceding account it is evident, (1) That in the embryo sheep at a certain stage of development, the dental lamina exists throughout the canine and incisor regions of the upper jaw. Its anterior portion, which is the LAST to develop and the first to abort, does not attain so prominent a condition as its lateral portion. After advancing in development for a time, it retrogrades and finally disappears. (2) That in the canine region the dental lamina gives rise to an enamel germ which never reaches a stage of functional activity; for neither are its central cells transformed into a stellate reticulum, nor do those of the malpighian layer ever produce enamel, and in later stages both disappear.

In this region there is no trace of a dentine germ. The fact of the existence in sheep of rudiments of such organs as usually result in the formation of teeth, is of interest because it is one of those peculiar structures for which it is difficult to account without the aid of the theory of natural selection. From the observations here recorded, one

readily sees that the disappearance of the superior incisors and canines is progressive. In the region of the incisors the evidences even of the beginnings of tooth development have almost disappeared, the region of the first incisor being the least differentiated portion of the tract, while the canine region is represented by a moderately large, but functionless enamel sac. Since in some ruminants destitute of incisors, small rudimentary canine teeth are found on the upper jaw of the adult animal, it is a fair inference that the teeth are being lost from before backward, and that the canine teeth, the last to disappear from the sheep, are in such cases undergoing degeneration, although not wholly functionless.

It is admitted that the history of the development of the individual reproduces, at least in part, the history of the ancestors of that individual, and that the changes in development take place in the same order as in the ancestors, then we have reason for believing that the progenitors of the ruminants possessed incisors and canine teeth on the upper jaw; that these teeth becoming, perhaps by a change in environment, no longer necessary for obtaining food, have gradually ceased to develop; and that the disappearance of the teeth has been a progressive process, beginning with the middle incisors and gradually involving the teeth farther back.

Cambridge, September, 1887.

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EXPLANATION OF FIGURES.

The following abbreviations are used in the figures.

cnn.	Canine.	*lng.*	Tongue.
crt. Mkl.	Meckel's Cartilage.	*l. lng.*	Lingual side.
e t.	Epithelium.	*md.*	Lower jaw (and os mandibularis).
g. de.	Dentine germ.		
g. cnn.	Enamel-organ germ of canine.	*ms d.*	Mesoderm.
g. en a.	Enamel-organ germ.	*mur.*	Plunging wall.
g. i'.	" " of first incisor.	*mx.*	Upper jaw (and os maxillaris).
g. i''.	" " second "	*n.*	Nerve.
g. i'''.	" " third "	*o. en a.*	Enamel organ.
g. pr. mol'.	" " first premolar.	*pr. mol.*	Premolar.
i.	Incisor.	*st. con.*	Stratum corneum.
la. de.	Dental lamina.	*st. Mpg.*	Stratum Malpighi.
l. lab.	Labial side.		

The average thickness of the sections is about 7.5 μ, and the number of each section in the series to which it belongs is indicated by the number in parenthesis adjacent to the number of the figure.

PLATE I.

Figures 1–25 are magnified 17 diameters; figures 26–29a, 11 diameters; figures 30–37, 175 diameters. All were drawn with the aid of the Abbe camera.

Figures 1–10 are from sections of the left side of the jaws of an embryo sheep, 37 mm. long, preserved with picrosulphuric acid, stained by means of Czoker's cochineal followed by alcoholic borax-carmine, imbedded in paraffine and mounted in Canada balsam. The figures all show the anterior face of the sections, which were so cut that the plane of the first section was parallel to the median plane of the head, the object being gradually rotated so as to keep the plane of the sections as nearly as possible perpendicular to the outer margin of the jaw.

Fig. 1 shows the plunging epithelial wall of the upper jaw, and the centre of the germ of the enamel organ of the first incisor on the lower jaw.

Fig. 2. On the lower jaw the section passes through the region between the first and second incisors, where only the dental lamina is to be seen. On the upper jaw the plunging wall is continued into the dental lamina without there

being any well-marked division between the two. They have a slightly different direction.

Fig. 3. A section through the middle of the region of the second incisor of the lower jaw. On the upper jaw the dotted line shows approximately the outline of the plunging wall of Fig. 1, as it would appear when projected on to the plane of this section. The portion beyond the dotted line is the dental lamina.

Fig. 4 is from a section about midway between the second and third incisors of the lower jaw.

Fig. 5 passes through the middle of the third incisor of the lower jaw.

Fig. 6 is from the region between the third incisor and canine tooth.

Fig. 7 shows the enamel germ of the canine tooth on the lower jaw. On the upper jaw the dental lamina can be distinguished from the plunging wall by its size and direction, as in the preceding figures.

Fig. 8. This section passes through the region between the canine tooth and the first premolar on the lower jaw. The dental lamina of the lower jaw no longer appears as an outgrowth from the epithelium of the plunging wall. The dental lamina of the upper jaw is much smaller than in the preceding sections.

Fig. 9 shows the middle of the enamel germ of the first premolar tooth of both jaws. The asterisk marks the position of a longitudinal ridge of epithelium near the base of the dental lamina.

Fig. 10. A section from the region between the first and second premolars. The dental lamina is pear-shaped in section throughout this region. The lateral ridges at the base of the dental laminæ are also continued through the greater part of the region.

Figs. 11–20 are sections through the left side of both jaws of a sheep embryo 56 mm. long, which was treated in the same manner as the embryo of 37 mm., with the exception that it was stained in Grenacher's borax carmine only. The sections were cut in the same manner as in the figures just described.

Figs. 11–15 are sections through the region of the first incisor of the lower jaw, showing the enamel germ of the first incisor as it appears in different regions. On the upper jaw the dental lamina and plunging wall are seen. Fig. 14 is through the centre of the enamel organ of the incisor.

Fig. 16 passes between the first and second incisors on the lower jaw. The dental lamina of the upper jaw has become broader, and its section therefore appears more elongated.

Fig. 17 passes through the middle of the second incisor on the lower jaw.

Fig. 18 shows the dental lamina in the regions between the second and third incisors.

Fig. 19. This section is taken through the centre of the enamel germ of the third incisor of the lower jaw.

Fig. 20 is through the middle of the enamel germ of the canine tooth of both jaws.

Figs. 21–25a are sections of the upper jaw of a sheep embryo 87 mm. long, treated in the same manner as the embryo 37 mm. long. The figures show the anterior faces of the sections through the upper jaw of the right side.

Fig. 21 shows the extent of the plunging wall and the dental lamina in a region opposite the middle of the first incisor of the lower jaw.

Fig. 22. The same in the middle of the second incisor region.

Fig. 23. The same in the middle of the third incisor region.

Fig. 23a shows the appearance seven sections further back than Figure 23.

Fig. 24 is a section behind the centre of the third incisor, showing a part of the dental lamina cut off from the buccal epithelium by the ingrowth of mesoderm.

Fig. 25 is a section through the middle of the canine region behind the region where there is a narrow connection of the enamel-organ germ with the buccal epithelium.

Fig. 25a. The enamel germ is divided by the deepening of a constriction shown in Figure 25 into two arms, the cross-sections of which appear in this figure as two isolated patches of epithelium.

Figs. 26–29a are sections through the left half of the upper jaw of an embryo sheep 112 mm. long, which was hardened in chromic acid and stained with Czoker's cochineal, followed by borax carmine. The sections were made in the same way as described in Figs. 1–10. They are magnified only 11 diameters.

Fig. 26 shows the condition of the plunging wall in the region opposite the first incisor of the lower jaw.

Fig. 26a shows the dental lamina more sharply marked off from the plunging wall as seen a few (18) sections further back than Fig. 26.

Fig. 27 is a section through the middle of the region opposite the second incisor of the lower jaw, showing a small but well defined dental lamina.

Fig. 28 shows the dental lamina in the region of the third incisor.

Figs. 29, 29a, are sections through the canine region.

Fig. 29 shows the rudimentary lamina to be still continuous with the buccal epithelium; but four sections further back it is detached from the "wall."

Fig. 29a. Back of the canine region the lamina is continued as a ridge or fold of epithelium, which soon changes from a horizontal to a vertical position.

PLATE II.

All figures of this plate are magnified 175 diameters.

Fig. 30. The deep portion of the dental lamina of Fig. 14. The change in the thickness of the malpighian layer is to be seen here, also its irregularity of outline.

Fig. 31 is a highly magnified view of the incisor region shown in Fig. 24. The difference between the differentiated and the undifferentiated portions of the lamina, which are here both surrounded by mesoderm, is well marked.

Fig. 32 gives a view of a portion of Fig. 25. The histological condition of the canine germ is the same as that of the differentiated portion of the dental lamina in Fig. 31.

Figs. 33–35 are from cross sections of the upper jaw of an embryo sheep 93 mm. long, which was treated with picrosulphuric acid and stained in borax-carmine

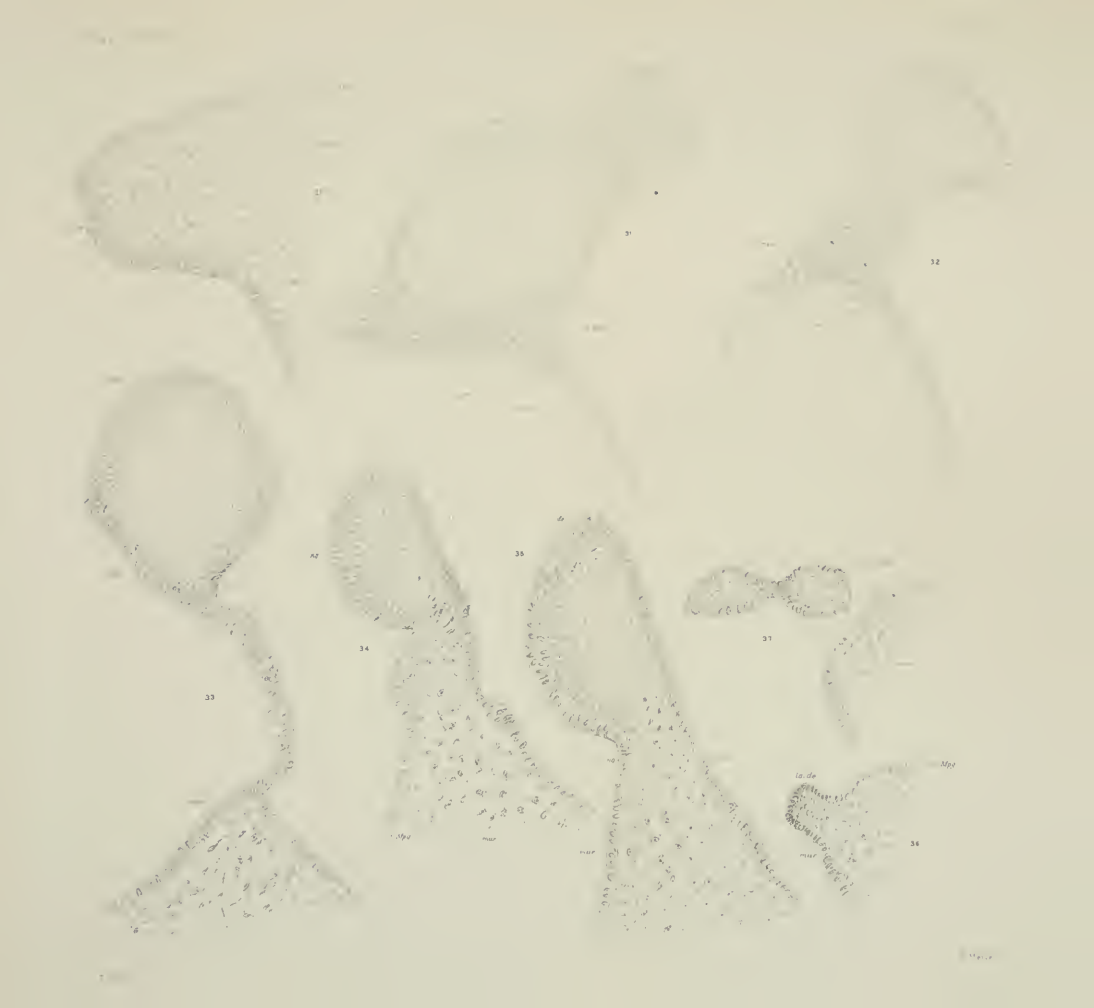
Fig. 33 is a section through the germ of the canine tooth. That portion of the neck of the germ which is nearest the buccal epithelium is resolved into a series of epithelial knots or islands.

Fig. 34 shows the condition of the lamina eight sections behind that shown in Fig. 35, still in the incisor region. The sections were 7.5 μ. thick.

Fig. 35 is the anterior face of a section through the incisor region, showing the condition of the dental lamina in the upper jaw.

Fig. 36. The dental lamina of Fig. 28 as it appears when highly magnified.

Fig. 37. A portion of the section outlined in Fig. 29a. The central cells of the germ have become vacuolated.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No. 10. — *The Rattle of the Rattlesnake.* By Samuel Garman.

The habit of sloughing is common to all the serpents. A short time before the removal takes place, the new epiderm makes its appearance beneath the old. Its presence is easily detected by a whitish color under the outer layer. The milky tint of the second layer extends over the whole body; on the eyeball it interferes greatly with the sight. During the time of its formation, several weeks, while the vision is affected, the snake prefers seclusion, and is disinclined to partake of food. Some days before casting, about a week in the most recent case followed, the milkiness vanishes, the skin resumes its ordinary aspect, and the sight becomes again as keen as formerly. By rubbing the lips the slough is loosened around the mouth, then it is pushed over the head to the neck, whence it is taken back over the body. From the neck backward it is, in some cases, removed by means of a coil or two of the tail, the body being crowded through and the epiderm left behind. A hole in the ground or between rocks, the sticks in a brush heap or the stalks in the grass, answer the same purpose as the ring made by the tail. Some manage to get the coat back until under the ventral scales, when the latter are used somewhat as in gliding, their free hinder edges catching and stripping off the slough as the body is moved slowly forward. From the hinder part of the body the removal is an easier matter: the loosened portion is caught around a stick or under a stone, and with a pull the balance is taken off in an instant. The slough comes away like damp paper; it is wet with a sticky mucus on the inner side, turned outward in the operation. The mode of growth and of removal is similar among the rattlesnakes. These snakes differ in retaining a portion of each slough, that covering the tip of the tail, to form one of the rings of the rattle. The attachment is purely mechanical; the rings are merely the sloughs of the end of the tail.

On the majority of the snakes, both the venomous and the non-venomous, the tail tapers more or less gradually to a point. At the end it is protected by a sub-conical cap of the epiderm. Under the latter lies the skin, and under it again the termination of the vertebral column, — a bone formed of vertebræ that have coalesced and changed

their shape until the outlines of the mass nearly resemble those of the surface of the tip. This terminal bone is hard externally, and cellular within; it contains and protects the extremities of the cord and vessels of the column in the positions occupied by them in the embryo before the consolidation was effected. In the different species the number of vertebræ included in this bone varies considerably; sometimes, also, it is seen to vary in individuals of the same species. Before the appearance of the scale-like folds on the tail of the embryo, the skin of the extremity is smooth; afterward, on some, the tip takes on the semblance of being protected on the sides by scales, the distal portions of which have blended with the cap, while their bases have remained distinct, much as if the conical envelope were still undergoing process of enlargement. In such cases the line of demarcation between the scales and the cap is irregular and indistinct. This condition obtains in species of Tropidonotus, Eutænia, Nerodia, and allies. The line of separation is very decided and regular in Crotalus. As the tail develops more slowly, the scales do not appear on it until after they are well formed on the body. Up to the time of their formation, the story of the caudal development of the rattlesnake is the same as that of any other serpent. The general shapes and the numbers of vertebræ differ greatly in the various kinds, but the history is similar in all. With the purpose of indicating the manner of growth of the rattle, and, as far as may be, of determining its origin, we shall have to follow it up through different species, a complete series of any one of them not being at hand.

Sistrurus, Garm. Figs. 1–4.

Crotalophorus, Gray, not of Linné.

S. miliarius, Linn., is the only rattlesnake of which we have a good series of the very early embryos. Some of these, already three inches in length, are not yet furnished with scales on the tail, though the entire body is well provided. Outwardly, in these specimens, the tail is short, thick, blunt, slightly compressed, and has no indication of the characteristic feature so prominent after birth. The vertebræ are separate.

Figures 1 and 2 of the diagrams are drawn from embryos of *S. catenatus*, Raf. (*Crotalus tergeminus*, Say), six and a quarter inches in length. Their only promise of the rattle is to be noted in the shape and size of the cap, or button. Upon the body the scales are perfect; the button evidently is incomplete, being little more than half of what it ultimately

becomes. If a button as it is at birth were to be cut through the constriction immediately behind the anterior swelling, the hinder portion would correspond with the cap as seen in Figures 1 and 2. There is no evidence of any fusion of scales with the button around its front border. Except in case of the button, there is externally very little difference between this stage and the next represented. Within the cap the vertebræ are distinct, slightly smaller than those just in front of them, like the latter surrounded by muscles, and the skin is thicker than elsewhere. Between this stage and the following the anterior portion of the cap appears to be added by backward growth at the front margin, like that which later in life displaces the older button to make way for the new.

Figures 3 and 4 are drawn from young ones of the same species, *S. catenatus*, Raf., eight and a quarter inches in length, about a week after birth. In them the button has been perfected, the cap having gained, as compared with Fig. 2, all the portion anterior to the constriction. On several of these specimens there is a tendency to fusion and irregularity among the scales immediately in front of the button, but in no case is there any disposition on the part of the scales to fuse with the latter. A portion of the button corresponding to the externally visible part of each ring has been acquired, while the entire length has increased a couple of inches, in a short time just before birth. Inside of the button the changes have been greater: the vertebræ, still plainly outlined, have consolidated into a single elongate mass, the size of which is being increased by both lateral and terminal growth; the vertical processes have grown together; and the muscles have been displaced by the enlarging bone and the thickening skin. Muscular command of the individual vertebræ within the button has been lost in the consolidation, but the muscles of the tail retain a firm hold on the mass, and the loss finds compensation in a better means of agitating the rattle. For later stages we are compelled to turn to a closely allied genus.

Crotalus, Linné.

Crotalophorus, Linn.; *Caudisona*, Laur.

Figures 5 and 6, from a *Crotalus confluentus*, Say, fourteen inches in length, show a considerable advance from the preceding. The specimen was taken, with the third button about half grown, when the process of pushing back the second ring was well under way. The first ring had

been set free with the first slough, holding only by the collar; and if the snake had been allowed to live a little longer, the second sloughing would have discovered the third button perfected, clasped by the second ring, the latter pushed back and loosened from the balance of the epiderm. Of the second ring the narrower posterior extension is quite empty; its anterior chambers are closely filled with the tumid skin, the loss of the ring being prevented in this manner, while the outer swelling of the new button is crowding it backward. A considerable shrinkage of the skin takes place after the moult; it is insufficient to allow the ring to slip off, though admitting of great freedom of motion. In front of the border of the second ring, Fig. 5, lies the fold, shrunken by alcohol in the specimen, by which the ring was displaced, and which was to become the largest chamber of the next succeeding. This fold is usually hidden by the epiderm attached to the ring, as in Fig. 6, until the operation of sloughing has been finished. The mass of bone occupies the place of eight or more of the vertebræ in this stage, the lines of separation being still noticeable to some extent. By a longitudinal section the cord and vessels are disclosed in their original positions, surrounded now by spongy bone, in which the cavities radiate from the centre toward the surfaces. On the upper and lower faces there is less indication of the composition.

Figures 7 and 8 were taken from a large specimen of *Crotalus horridus*, Linn. In it the traces of the vertebræ in the terminal bone are almost obliterated; the bone has thickened, pushed forward at the edges, and otherwise enlarged. Along with this there has been an excessive development of the muscles of the tail. The rattle is entire, of eleven rings and a button. The hinder seven of the rings belong to the period of the snake's most rapid growth; they form the "tapering rattle" common to the young individuals, formerly used in classification of the species by some authors. Four of the rings and the button pertain to a part of the creature's life in which the gain in size was much less rapid; they form the "parallelogramic rattle" of the same writers. The mistaken use of these features in specific diagnoses no doubt arose from study of incomplete rattles. The change from the taper to the more nearly parallelogramic takes place about the seventh ring, — in *Sistrurus miliarius* often with the sixth, with the larger species frequently with the eighth, — and affords the means of obtaining an approximate idea of the comparative age of the owner of the series of rings. The figures show the rattle as commonly held by the snake when crawling. In a single series of rings there is much variation in

shapes, as in sizes, and there are also considerable differences in the rattles within the species. In the case of the small snake *Crotalus exsul*, Garm., from Cedros Island, Lower California, the large size of the first ring is evidence of derivation from a larger species, probably *C. lucifer*, B. & G., of the mainland. In this case, the change in button has not kept pace with the reduction in size of body, or the changes in squamation, etc. While the rings vary with rapidity of growth in the body, from amount of food, it is unlikely that it makes any difference in their number, or that of the sloughings.

More than seventy specimens have been looked over for evidence of growth of a new button between the months of May and September; two, and a doubtful third, favor the conclusion that a ring is added in the fall. One of these, as it was in September, is sketched in Figures 5 and 6. On the other hand, living specimens kept through the winter prove that a new growth does take place toward spring, and that when the epiderm is shed, on coming out of winter quarters, the animal is possessed of an addition to the rattle.

The mechanism of the organ has been so often described and figured that it is unnecessary to give a detailed description here. Among the most accurate of the earlier writers is Lacépède, 1789 (Histoire des Serpens, II. pp. 390–420, Pl. XVIII.); and of the more recent, Czermak, 1857 (Ueber den schallerzeugenden Apparat von Crotalus, in Vol. XIII. of the Zeitschrift für wissenschaftliche Zoologie, pp. 294–302, Pl. XII.). For comparison with what has been recorded above, a few sentences are quoted from Lacépède (p. 404). Speaking of the mode of growth, he says: "Quand une pièce est formée, il se produit au-dessous une nouvelle pièce entièrement semblable à l'ancienne, et qui tend à la détacher de l'extrémité de la queue. L'ancienne pièce ne se sépare pas cependant tout-à-fait du corps du serpent; elle est seulement repoussée en arrière; elle laisse entre son bord et la peau de la queue, un intervalle occupé par le premier bourlet de la nouvelle pièce; mais elle enveloppe toujours le second et le troisième bourlets de cette nouvelle pièce, et elle joue librement autour de ces bourlets qui la retiennent. . . . Si les dernières vertèbres de la queue n'ont pas grossi pendent que la sonnette s'est formée, chaque pièce qui s'est moulée sur ces vertèbres a le même diamètre; et la sonnette paroit d'une égale largeur jusqu'à la pièce qui la termine; si, au contraire, les vertèbres ont pris de l'accroissement pendant la formation de la sonnette, les bourlets de la nouvelle pièce sont plus grands que ceux de la pièce plus ancienne, et le diametre de la sonnette diminue vers la pointe."

The anatomy of Crotalus was studied by Tyson in 1683 (Philosophical Transactions, No. 144).

In regard to the use of the rattle there is not much to be said. Mainly, it is used to warn off disturbers, and thus prevent useless expenditure of venom. Success in capture of food depends on an ever ready supply of poison. To secrete a new lot takes time. The rattle is used also in breeding season, though it is doubtful if the dull-eared creatures depend on sound, rather than scent, to find their mates. A theory advocated by some maintains that the organ is used in imitating insects, to draw the birds. An objection to this is the fact that birds are somewhat rarely found in stomachs of the Crotali. An observation appearing to favor this theory was made on a Dakota snake, found braced up among the branches of a sage bush in such a way that the head overlooked the surrounding bushes, while the tail, within the mass of branchlets, was free to keep up the rattling that attracted the attention of a party more than fifty yards distant. But the approach of the troop may have occasioned the creature's peculiar behavior.

Origin of the Rattle.

Many serpents besides those possessed of a crepitaculum are addicted to making a rattling noise by vibrations of the end of the tail. It is likely the modifications of the organ apparent in some or others of these are consequences of this habit. In illustration of the extent to which the tail has been modified in different cases, apparently for similar purpose, attention is directed to Figures 9–14, from species allied to the rattlesnakes.

Rhinocerophis ammodytoides, Leybold, Figs. 9, 10, from the Argentine Confederation, has its most prominent distinguishing features in a prominence on the top of the snout, and, of more importance in this writing, a peculiar termination of the tail. Fig. 9 outlines the caudal surface. The terminal piece is sub-crescentic in longitudinal vertical section, and sub-round in transverse. Externally it is covered by the horny skin, internally it is bony. On the top, two of the dorsal scales reach back more than a third of the length, and near their tips fuse with each other and the skin about them. Fig. 10 shows the arrangement after the skin and muscles have been removed. The outside of the bone is hard, the inside not solid. It is penetrated by the canals of the vertebræ, — indications of its origin. Inferiorly, it extends forward below three of the vertebræ, firmly anchylosed to it and to each other,

the anterior of the three being partly subtended. In front of it, the column is normal. Each vertebra is long, low, rather broad, and vertically crossed in the middle by a light line, as if two had joined end to end. The neural spines are low, inclined backward, and, in the hinder three or four, expanded laterally on the upper edge into a flange that in the posterior unites with the terminal bone. Zygapophyses and parapophyses are feebly developed; the hypapophyses are blade-like, thin, and fragile. Appearances suggest that the tip is carried upon and struck against the ground.

On *Lachesis mutus*, Linn., Fig. 11, from Brazil and Northern South America, the end of the tail is a long, slender, compressed, cultriform blade. The scales in front of it are small and tubercular. This is especially the case with a dozen or more of the sub-caudals, that, as they approach the end, are subdivided and spine-like. Within the cap the bone is similar to those described above. The vertebræ preceding it are slender, with weak processes. Near the extremity the tail is slender and very flexible, a condition enhanced by the smallness of the scales. It looks as if it were carried off the surface.

Halys acutus, Gth., Fig. 12, is a serpent recently described by Dr. Gunther, 1888 (Ann. Mag. Nat. Hist., (6), I. 171, Pl. XII.), from the mountains north of Kiu Kiang, China. It is remarkable on account of a flexible pointed lobe extended from the end of the snout, and for the peculiar scutellation of its compressed tail. Dr. Gunther says the tail is not to be in any way taken as an initial step in the development of the rattle of Crotalus, though the organ in this species may in a much smaller degree exercise the same function as in the rattlesnake, being an instrument by which vibrations and sound are produced. From what we have seen above, it is not difficult to imagine a rattle developed from the arrangement of scales and vertebræ present in this snake. However, as Dr. Gunther remarks, and as illustrated below, it is quite unnecessary to suppose the tail of Crotalus has gone through such modification.

Ancistrodon piscivorus, Holbr., Fig. 13, the Moccasin, from the Southern United States, is similar to Rhinocerophis in the structure of the tip. The terminal bone is not so greatly developed. A greater number of scales have fused with the cap.

On *Ancistrodon contortrix*, Linn., Fig. 14, the Copperhead, of the United States to Mexico, the tip differs a little from that of its congener, the Moccasin; it is directed downward as well as backward. Most often the cap, or button, has one or two swellings in a degree resembling those

on a ring of the rattle. A living specimen of this snake, kept for a year or more, would take to rattling on the floor whenever he was irritated. The sound was made by the terminal inch of the tail, this part being swung from side to side in the segment of a circle, so that the tip might strike downward. The result was a tolerable imitation of that made by a small rattlesnake.

Both Copperhead and Moccasin bear evidence of union between cap and scales. All the specimens have two scales fused above and two below the button; some show that more have joined the two above, and that one or more of the laterals has been included on the sides.

The testimony of the embryo is to the effect that the rattlesnakes were derived from forms in which the terminal vertebræ were not fused into a terminal bone. There seems to be no radical difference, in the earlier stages of the end of the tail, between the above mentioned as well as other non-crotalophorus forms and Crotalus. So much divergence in the number and shape of the caudal vertebræ occurs in the various genera, that these features become matters of secondary interest in a general comparison. In the later development the rattlesnake goes farther than any of the others. The bone at the end of the column is of the same nature throughout the Ophidia. On Crotalus it eventually contains a greater number of vertebræ, there is a greater enlargement of the mass, and in devoting it exclusively to shaking the rattle, instead of striking upon objects, a different use is made of it. In front of the rattle the neural spines incline forward, possibly a consequence of the function of the tail. This inclination has little weight when compared with forms like Ancistrodon, where the spine is so low. Similar leaning toward the head occurs in the Hydrophidæ and in Ogmophis, a Tertiary fossil of uncertain affinity. So far as the vertebræ are concerned, they point to no special one of the recent allies as representative of the stock from which the rattlesnakes have sprung.

With the button there is but little more success. While it might possibly have been formed or enlarged by fusion of scales with the cap, there is really no reason to suppose scales were formed on the end of the tail only to be lost again. In fact, embryonic data favor the conclusion that it was formed by simple enlargement, or expansion of the cap itself. A cap that by its shape would be mechanically held to its successor might be produced by slight changes in that of any one of a number of species of the family, in addition to those figured. Shape is the important feature in the retention of the series of caps. This, in the

rattlers, is obtained through that of the end bone, the thick skin covering the latter, and the mode of growth. Generally, on the pointed tip there is no chance to retain the cap during and after the slough. Without the backward growth from the front border at the time of forming the cap, again, the rattle would not exist, as each new cap would be formed entirely within its predecessor. *Ancistrodon contortrix*, the Copperhead, Fig. 14, gives a hint of the probable manner of origin of the rattle, in the folds, or swellings, at the front border of the cap. The presence of these folds apparently indicates that growth from the margin has taken place. If, as seems to be the case from the folds, the necessary manner of growing already exists, but a slight increase in it, increasing the amount of the swellings and constrictions, would be needed to provide the Copperhead with a rattle. After the retention of the displaced cap was secured, the change from the habit of striking the tip upon the ground to simple shaking would be followed by loss of flexibility in the tail itself, by rigidity of the column, — a condition, with inclusion in the cap and the peculiar strain on the muscles, favoring consolidation of the terminal vertebræ, and tending to draw the spines forward. It appears very much as if the rattle originated in some such way.

Though the Copperhead has been specially used as an illustration here, it is not asserted that the rattlesnakes are directly derived from it. Taking the general characteristics into consideration, it seems more likely they took origin in several stocks; one of them, allied rather closely to Ancistrodon, yielding the Sistruri (the small rattlesnakes with large crown shields); another, nearer to Lachesis, giving rise to *Crotalus durissus* and allies.

In summarizing, we may say the rattlesnakes have probably been derived from members of the same family that had no rattle. The button of the rattle was formed by enlargement of the terminal cap covering the terminal bone, very likely without fusion with scales. The shape of the button was determined by that of the bone and skin of the tip; it is modified in the second and following rings by the ring immediately preceding. The exterior or exposed part of each button after the first, is formed in front of the ring with which it is in contact, and pushes the latter back. As the button is displaced to become a ring, it is prevented from passing entirely off by the swollen skin, completely filling its anterior chambers, behind the constrictions. The development of the button and the rattle was accompanied by a consolidation and compacting of a larger number of the vertebræ, with loss

of the muscles directly belonging to the reduced portion, and with greater development of the muscles in front of it. And, finally, the probability that the rattlesnakes represent at least two lines of descent may be added; one, that of Sistrurus, more closely connected with the Copperheads; another, that of *Crotalus durissus* and allies, connecting with that of *Lachesis mutus*.

April 16, 1888.

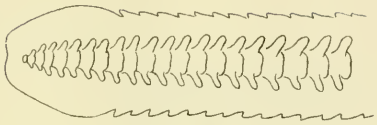
LIST OF DIAGRAMS.

PLATE I.

Figs. 1, 2. Sistrurus catenatus. 4 times nat.
3, 4. Sistrurus catenatus. 3½ times nat.
5, 6. Crotalus confluentus. 2 times nat.
7. Crotalus horridus. Nat. size.

PLATE II

Fig. 8. Crotalus horridus. Nat. size.
9, 10. Rhinocerophis ammodytoides. 2½ times nat.
11. Lachesis mutus. 3 times nat.
12. Halys acutus. After Günther.
13. Ancistrodon piscivorus. 2 times nat.
14. Ancistrodon contortrix. 2½ times nat.



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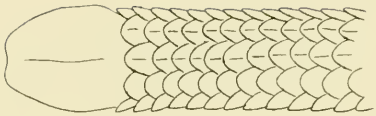

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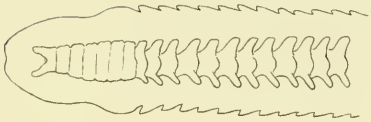

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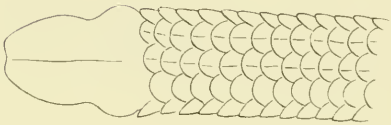

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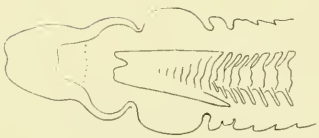

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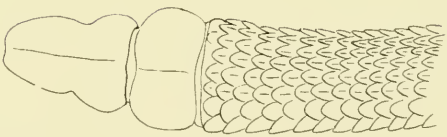

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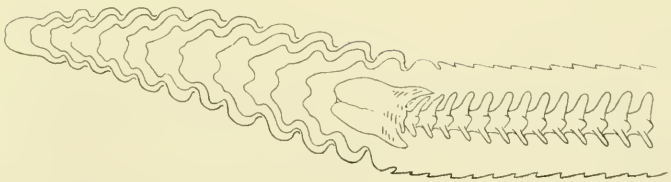

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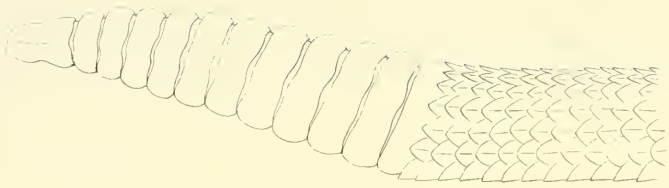
B. Meisel, lith. Boston



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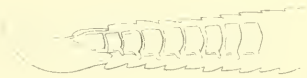

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